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DEGREE FOR WHICH THESIS WAS PRESENTED . . . . . Doctor of Philosophy

YEAR THIS DEGREE GRANTED 1983

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A COMPARISON OF THREE ALGAL COMMUNITIES IN A PRAIRIE-PARKLAND LAKE

by

CHARLES GARY JENKERSON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

ALGAL ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING, 1983

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance a thesis entitled "A COMPARISON OF THREE ALGAL COMMUNITIES IN A PRAIRIE-PARKLAND LAKE" submitted by Charles Gary Jenkerson in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Algal Ecology.

ABSTRACT

The phytoplankton, epipelon, and epiphyton of a eutrophic prairie-parkland lake have been characterized by spatial and temporal distributions of abiotic and biotic parameters. Comparisons of the three communities were facilitated by simultaneous collection and similar processing.

For all communities the 1% surface irradiance was at 1-2 meters due to shading algae, macrophytes, and wind mixed detritus, or due to ice and snow cover. Distributions of abiotic parameters were similar among communites. Temperatures in the epipelon were less rigorous than those in the phytoplankton, whereas temperatures in the epiphyton were more rigorous. For pH and orthophosphate, epiphyton > phytoplankton > epipelon. Alkalinity was epipelon > phytoplankton > epiphyton. Epipelic silica was highest. Relative nitrate concentrations were not consistent.

For species diversity, phytoplankton > epiphyton > epipelon. Vertical distributions were noted for species within each community. Dominant species from the phytoplankton and epiphyton were restricted within seasonal shock period boundaries, but dominants from the epipelon trespassed such environmental boundaries. There were 21 dominant species considered community indicators. But 19 species were dominant and at least common in more than one community. Evidence suggested the epiphyton can be a collection site for senescing populations from all communities, but it also can act as an incubator site where sufficient light, heat, and nutrients

initiate species growth that later is expressed in another community. Likewise the epipelon can be a disposal site for senescent populations, but it too can be a stable maintenance site where species from all communities survive, or even display active growth.

Standing crop and productivity data showed similar spatial and temporal distributions for all communities. Relative to total lake summation, the phytoplankton > epiphyton > epipelon, and the potential importance of the epiphyton was noted. Interactions among the three communities were indicated as an orderly progression of first phytoplankton, then epipelon, and finally epiphyton peaks occurred within each season. The photosynthetic index, photosynthetic efficiency, and productivity efficiency for all communities showed similar spatial but variable temporal distributions. The photosynthetic index and efficiency were highest for the phytoplankton, and the productivity efficiency was highest for the epiphyton.

ACKNOWLEDGEMENTS

Dr. M. Hickman was mentor and friend throughout the course of this study. His varied scientific and cultural background provided much in the way of technical assistance and personal interest. I wish to extend my sincerest respect and appreciation for his guidance and perseverance.

I want to express my gratitude to all those who provided computer services from Southeast Missouri State University and The University of Alberta, and chemical analyses from Alberta government laboratories and The University of Alberta laboratories. Special mention is given to Gertie Hutchinson and Marianne Klemka, water chemistry technicians from The University of Alberta, who put hours of conscientious effort into this study.

My warmest regards go to fellow students Dave Beliveau, Rod Forbes, Rob Baker, and Dr. Dave Potter. Their ability to immerse themselves in their work and still maintain contact with others was an inspiration to me. Of special note too in this respect was Fred Rourke, a long time resident at Hastings Lake. With his personable nature, he offered food, lodging, and invaluable conversation. He made my field experience a remarkable opportunity.

Most importantly, I want to recognize my family whose encouragement and good cheer was undaunted.

I acknowledge financial support provided by Graduate Teaching Assistanceships from the Department of Botany, a Dissertation Fellowship from The University of Alberta, and an operating grant to Dr. M. Hickman (A6384) from the National Research Council.

TABLE OF CONTENTS

CHAPTER PAGE

1. INTRODUCTION 1

2. DESCRIPTION OF LAKE 3

2.1. Location and Geology 3
2.2. Climate and Vegetation 6
2.3. Morphology 6

3. PHYTOPLANKTON 9

3.1. Methods 9

3.1.1. Physico-chemical Parameters 12
3.1.2. Species 14
3.1.3. Chlorophyll a 15
3.1.4. Productivity 16
3.1.5. Cross Incubation Studies 16
3.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 17

3.2. Results 17

3.2.1. Physico-chemical Parameters 17
3.2.2. Species 36
3.2.3. Standing Crop 49
3.2.4. Productivity 59
3.2.5. Cross Incubation Studies 61
3.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 72

3.3. Discussion 77

3.3.1. Physico-chemical Parameters 77
3.3.2. Species 85
3.3.3. Standing Crop 92
3.3.4. Productivity 96
3.3.5. Cross Incubation Studies 102
3.3.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 104

4. EPIPELON 108

4.1. Methods 108

4.1.1. Physico-chemical Parameters..... 111
4.1.2. Species 114
4.1.3. Chlorophyll a 114
4.1.4. Productivity..... 115

4.1.5. Cross Incubation Studies 115
4.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 116

4.2. Results 116

4.2.1. Physico-chemical Parameters 116
4.2.2. Species 119
4.2.3. Standing Crop 130
4.2.4. Productivity 142
4.2.5. Cross Incubation Studies 142
4.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 145

4.3. Discussion 151

4.3.1. Physico-chemical Parameters 151
4.3.2. Species 152
4.3.3. Standing Crop 160
4.3.4. Productivity 162
4.3.5. Cross Incubation Studies 163
4.3.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 164

5. EPIPHYTON 166

5.1. Methods 166

5.1.1. Physico-chemical Parameters 170
5.1.2. Species 171
5.1.3. Chlorophyll a 171
5.1.4. Productivity 172
5.1.5. Cross Incubation Studies 172
5.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 173

5.2. Results 173

5.2.1. Physico-chemical Parameters 173
5.2.2. Species 180
5.2.3. Standing Crop 191
5.2.4. Productivity 191
5.2.5. Cross Incubation Studies 194
5.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 202

5.3. Discussion 202

5.3.1. Physico-chemical Parameters 202
5.3.2. Species 205
5.3.3. Standing Crop 213
5.3.4. Productivity 215

5.3.5. Cross Incubation Studies 216
5.3.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 217

6. COMPARISON OF ALGAL COMMUNITIES 218

6.1. Results 218

6.1.1. Physico-chemical Parameters 218
6.1.2. Species 228
6.1.3. Standing Crop 240
6.1.4. Productivity 249
6.1.5. Cross Incubation Studies 255
6.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 255

6.2. Discussion 257

6.2.1. Physico-chemical Parameters 257
6.2.2. Species 260
6.2.3. Standing Crop 263
6.2.4. Productivity 264
6.2.5. Cross Incubation Studies 266
6.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency 266

7. BIBLIOGRAPHY 268

LIST OF TABLES

TABLE	DESCRIPTION	PAGE
1.	Morphometric features of Hastings Lake.	8
2.	Physico-chemical parameters. Ion concentrations are in mg/l.	18
3.	Dominant species found in the phytoplankton.	37
4.	Means of photosynthetic index, photosynthetic efficiency, and productivity efficiency tabulated depth by depth for the phytoplankton, during the May through October period of 1975.	73
5.	Dominant species found in the epipelon.	120
6.	Mean primary productivity, photosynthetic index, photosynthetic efficiency, and productivity efficiency, during the May through October period of 1975 for the epipelon.	150
7.	The mean and standard deviation of pH, total alkalinity, dissolved silica, nitrate-nitrogen, and phosphate-phosphorus at each site for 1974 data from the epiphyton.	174
8.	Dominant species for the epiphyton.	181
9.	Mean photosynthetic index, photosynthetic efficiency, and productivity efficiency by depth in the epiphyton.	199
10.	Means and standard deviations for May through October chemistry data of the phytoplankton, epipelon, and epiphyton.	222
11.	Dominant algae from the phytoplankton (P), epipelon (E), and epiphyton (EP). Dominant > 20% of the total community cell counts on any given sampling date, Common > 1 %, Present < 1%.	229, 230
12.	Percent composition of algal divisions in the phytoplankton, epipelon, and epiphyton.	239
13.	Standing crop chlorophyll a for each algal community at 0 m, in the 0 to 1 m littoral zone, and on a total lake basis.	244
14.	Productivity data for each algal community at	

0 m, in the 0 to 1 m littoral zone, and on a total lake basis. 250

15. Photosynthetic index, photosynthetic efficiency, and productivity efficiency data for each algal community. 256

LIST OF FIGURES

FIGURE	DESCRIPTION	PAGE
1.	Bathymetric map of Hastings Lake. Depth contours are drawn in meters.	5
2.	Bathymetric map of Hastings Lake with phytoplankton sampling station for 0, 1, 2, 3, 4, 5, 6, and 7 m depths indicated.	11
3.	Time-depth diagram of lake water temperature in °C (A) and time-depth diagram of percent saturation oxygen (B) for the phytoplankton.	21
4.	Time-depth diagram of pH (A) and time-depth diagram of conductivity expressed as micromhos/cm (B) for the phytoplankton.	26
5.	Time-depth diagram of mg calcium/l (A) and time-depth diagram of mg sulfate/l (B) for the phytoplankton.	28
6.	Time-depth diagram of meq bicarbonate (A) and time-depth diagram of mg silica/l (B) for the phytoplankton.	30
7.	Time-depth diagram of mg nitrate/l x 10^2 (A) and time-depth diagram of mg orthophosphate/l x 10^2 (B) for the phytoplankton.	32
8.	Seasonal distribution of *Anabaena circinalis* depth by depth for the phytoplankton.	40
9.	Seasonal distribution of *Rhodomonas minuta* depth by depth for the phytoplankton	42
10.	Seasonal distribution of *Selenastrum minutum* depth by depth for the phytoplankton.	44
11.	Seasonal distributions of A. *Merismopedia tenuissima*, B. *Anabaena flos-aquae*, C. *Aphanizomenon flos-aquae*, D. *Microcystis aeruginosa*, E. *Coelosphaerium naegelianum*, F. *Oscillatoria subbrevis*, G. *Gomphosphaeria lacustris* var. *compacta*, H. *Stephanodiscus hantzschii*, I. *Crucigenia quadrata*, J. *Botryococcus sudeticus*, K. *Chlorella vulgaris* L. *Kirchneriella contorta*, M. *Chlamydomonas* spp. N. *Gonium sociale*, and O. *Pandorina morum* for the phytoplankton.	46

12. Seasonal distribution of algal divisions expressed on a percent composition basis (A) and seasonal distribution of species richness S, evenness E, and Shannon's diversity H (B) for the phytoplankton. 51

13. Relationship between mg chlorophyll a/m^3 and total cells/ml x 10^3 for the phytoplankton. 53

14. Time-depth diagram of mg chlorophyll a/m^3 for phytoplankton 1974/1975 (A) and 1975/1976 (B). Time-depth diagram of mg carbon/hr/m^3 for phytoplankton 1975/1976 (C). 55

15. Phytoplankton productivity (A) and photosynthetic index (B) as a function of collection and suspension depths for October 1975 through January 1976. 63

16. Phytoplankton productivity (A) and photosynthetic index (B) as a function of collection and suspension depths for March through June 1976. 65

17. Phytoplankton productivity (A) and photosynthetic index (B) as a function of collection and suspension depths for August through September 1976. 67

18. Seasonal distribution of photosynthetic index (_____) and photosynthetic efficiency (- - - -), and productivity efficiency(.....) based on 0 m data for the phytoplankton. 75

19. Bathymetric map of Hastings Lake showing sampling stations for the epipelon at 0 (0.25), 2, 3, 4, 5, 6, and 7 m depths. 110

20. Vertical distribution of percent organic carbon in sediments and percent light attenuation (A), of temperature and percent saturation oxygen (B), of species richness S, evenness E, and Shannon's diversity H (C), and algal divisions for 1974 (D), 1975 (E), and 1976 (F) in the epipelon. 113

21. Seasonal distribution of incident irradiance in gcal/cm^2/day, lake water temperature in °C, depth of euphotic zone as 1% incident irradiance, mg phytoplankton chlorophyll a/m^3, pH, bicarbonate as mg carbon/l, mg silica/l, mg nitrate/l, mg orthophosphate/l, and mg oxygen/l for the epipelon. 118

22. Seasonal distribution depth by depth of *Navicula cryptocephala*, *Navicula gracilis*, and *Navicula hungarica* var. *capitata* for the epipelon. 122

23. Seasonal distribution depth by depth of Achnanthes sp., Nitzschia gracilis, and Nitzschia palea for the epipelon. 124

24. Seasonal distribution depth by depth of Oscillatoria subbrevis, Trachelomonas granulosa, and Anabaena flos-aquae for the epipelon. 126

25. Seasonal distribution for mean of 7 depths for Merismopedia tenuissima, Microcystis aeruginosa, Merismopedia glauca, Coelosphaerium naegelianum, Lyngbya lagerheimii, Pediastrum boryanum, Chlorella vulgaris, Crucigenia quadrata, Dictyosphaerium pulchellum, and Chlamydomonas spp. in the epipelon. 129

26. Seasonal distribution of algal divisions expressed as $\log_{10}$ cell counts/m^2 (A) and as percent composition (B) for the epipelon. T = total cells; Cy = Cyanophyta; B = Bacillariophyta; Ch = Chlorophyta; E = Euglenophyta. 132

27. Seasonal distribution of number of species present, evenness, and Shannon's diversity for the epipelon. 134

28. Vertical distribution of standing crop chlorophyll and cell counts for the epipelon. 136

29. Vertical distribution of standing crop chlorophyll, cell counts, and productivity for the epipelon. 138

30. Seasonal distribution depth by depth of standing crop chlorophyll and cell counts for the epipelon. 140

31. Seasonal distribution depth by depth of mg chlorophyll a/m^2 and mg carbon/hr/m^2 (A). Seasonal distribution of the photosynthetic index C/Ch a, photosynthetic efficiency C/L, and productivity efficiency C/(Ch a x L) based on 0 m data (B) for the epipelon. 144

32. Productivity for the epipelon expressed as a function of collection and incubation depths. 147

33. Photosynthetic index for the epipelon expressed as a function of collection and incubation depths. 149

34. Bathymetric map of Hastings Lake showing sampling sites for the epiphyton EP1, EP2, EP3, EP4, and EP5. 168

35. Seasonal distribution of pH, alkalinity as mg $CaCO_3$/l, mg SiO_2/l, mg NO_3/l, mg PO_4/l, mg O_2/l, temperature °C, surface irradiance in gcal/cm^2/day,

euphotic zone depth as 1% surface irradiance, and mg chlorophyll a/m phytoplankton for the epiphyton. 176

36. Vertical distribution of % irradiance (I) based on 100% surface irradiance in pelagial zone, of % oxygen saturation (O), and of temperature (°C) in graph A; vertical distribution of % algal divisions in graph B; and vertical distribution of species richness (---S---), of species evenness (_ _ E _ _), and of Shannon's diversity (__H__) for the epiphyton. 179

37. Seasonal distribution of Lyngbya diguetii, Oscillatoria subbrevis, Rivularia haematites, Calothrix species, Merismopedia tenuissima, Anabaena flos-aquae, Microcystis aeruginosa, Coelosphaerium naegelianum, Stigeoclonium nanum, Chlamydomonas species, Cocconeis placentula, Nitzschia species, Rhoicosphenia curvata, Cyclotella meneghiniana, Gomphonema parvulum, and Synedra acus per m² host stem for the epiphyton. 183

38. Vertical distributions of Stigeoclonium nanum (____), Lyngbya diguetii (- - -), and Calothrix spp. (.....) per m² host stem for the epiphyton. 185

39. Vertical distributions of Cocconeis placentula (____), Rhoicosphenia curvata (- - -), and Gomphonema parvulum (.....) per m² host stem for the epiphyton. 188

40. Seasonal distribution of percent composition for algal divisions in graph A, of cell counts for algal divisions and total cells in graph B, and of species richness (---S---), species evenness (____E __ __), and Shannon's diversity (__H__) in graph C for the epiphyton. 190

41. Vertical distribution of cell counts per m² host stem (-----), mg chlorophyll a per m² host stem (_ _ _), and mg carbon per m² host stem per hour (____) for the epiphyton. 193

42. Seasonal distribution of cell counts per m² host stem (____), mg chlorophyll a per m² host stem (_ _ _), and mg carbon per m² host stem per hour (.....) for the epiphyton. 196

43. Epiphyton productivity expressed as a function of collection and incubation depth. 198

44. Epiphyton photosynthetic index expressed as a

function of collection and incubation depth. 201

45. Seasonal distribution of the photosynthetic index, photosynthetic efficiency, and productivity efficiency for the epiphyton. 204

46. Seasonal distribution of surface irradiance, depth of 1% surface irradiance, temperature, and oxygen; seasonal distribution of pH, mg/l calcium carbonate, mg/l silica, mg/l nitrate, and mg/l orthophosphate for the phytoplankton (_____), the epipelon (----), and the epiphyton (__.__.__). 220

47. Seasonal distribution of diatom populations from the phytoplankton (_____), the epipelon (-----), and the epiphyton (__.__.__) along with that of mg/l silica (------). 225

48. Log_{10} total lake diatoms graphed against the reciprocal of mg/l silica. 227

49. Seasonal distribution of Anabaena flos-aquae, Microcystis aeruginosa, Coelosphaerium naegelianum, Merismopedia glauca, Merismopedia tenuissima, Lyngbya lagerheimii, and Oscillatoria subbrevis for the phytoplankton (_____), the epipelon (_ _ _), and the epiphyton (__.__.__). 232

50. Seasonal distribution of Pediastrum boryanum, Gonium sociale, Ankistrodesmus falcatus, Crucigenia quadrata, Dictyopsphaerium pulchellum, Chlorella vulgaris, and Chlamydomonas spp. for the phytoplankton (_____), epipelon (_ _ _), and epiphyton (__.__.__). 235

51. Seasonal distribution of Trachelomonas granulosa, Cyclotella meneghiniana, Stephanodicus hantzschii, Nitzchia spp., and Navicula cryptocephala for the phytoplankton (_____), epipelon (_ _ _), and the epiphyton (__.__.__). 238

52. Seasonal distribution of species richness S, species evenness E, and Shannon's diversity H for the phytoplankton (_____), epipelon (_ _ _), and epiphyton (__.__.__). 242

53. Seasonal distribution of ln standing crop chlorophyll a for total lake phytoplankton (_____), total lake epipelon (_ _ _), total lake epiphyton (__.__.__), and total lake summation (_____). 246

54. Seasonal distribution of 0 m data for phytoplankton mg

chlorophyll a/m^3 (_____), epipelon mg chlorophyll a/m^2 (_ _ _), and epiphyton mg chlorophyll a/m^2 (__.__.__). .. 248

55. Seasonal distribution of $\log_{10}$ mg carbon/hr for total lake phytoplankton (_____), total lake epipelon (_ _ _), total lake epiphyton (__.__.__), and total lake summation (_____). 252

56. Seasonal distribution of 0 m data for phytoplankton mg carbon/m^3/hr (_____), epipelon mg carbon/m^2/hr (_ _ _), and epiphyton mg carbon/m^2/hr (__.__.__). 254

1. INTRODUCTION

The comparison of algal communities has long been of interest in aquatic ecology. Before algal communities were generally recognized as working units, species lists were juxtaposed (e.g. Godward 1937). This eventually grew into the more elegant mapping of species travel from community to community within a single lake (Lund 1954, 1955, Jorgensen 1957). However, the intriguing idea of species cycling through one community to another was shown not to be true generally, and instead, a minimal species inocula maintained within each community seemed an integral part of the algal community concept (Round 1965a). Subsequent comparative studies tended to stress the integrity of community dominant species and the transience of community casual species (Brown and Austin 1973).

Some other subjects of intercommunity studies have not been as persistently persued. Valid but largely unnoticed references have been made to intercommunity competition for light (Moss 1969a,b, Straskraba and Pieczynska 1970), for nutrients (Jorgensen 1957, Brandl, et al. 1970), and for stimulatory, or inhibitory, organic exudates (Guseva and Goncharova 1965, Kogan and Chinnova 1972).

Of more significant interest has been the relative input of communities to total lake standing crop and productivity in terms of lake management. In the past, this has meant collating studies on individual communities and interpreting methods. However, there now exist generally accepted techniques which determine areal standing

crop and productivity for both the phytoplankton and the benthic algal communities through chlorophyll *a* analysis and carbon-14 procedures. These relatively quick and meaningful methods have encouraged the congruent collection of several sets of data from more than one community. A few studies then have encompassed the beginnings of valid community comparisons by presenting annual means of standing crop and productivity ascertained simultaneously for more than one algal community within a single lake ecosystem (Straskraba 1963, Wetzel 1964, Efford 1967, Hargrave 1969, Gruendling 1971, Gak, *et al*. 1972, Wetzel, *et al*. 1972, Winberg, *et al*. 1972, Schindler, *et al*. 1973, McCracken, *et al*. 1974, Adams and McCracken 1974). Now too, studies of seasonal interrelationships have suggested community spatial and temporal adaptations evolved through intercommunity competition (Clark and Runnels 1975, Komarkova and Komarek 1975, Kowalzcewski 1975, Kairesalo 1976, Moss 1977).

This study of the phytoplankton, epipelon, and epiphyton in a prairie-parkland lake adds to that setting. It is felt that each community is of note in and of itself because the lake is not stratified and is subject to ice cover virtually six months of the year. Therefore, a separate chapter is devoted to each community, characterizing the spatial and temporal distributions of species, standing crop, and productivity. However, more importantly, the communities have been sampled and processed simultaneously in as like a manner as possible. This facilitates the comparison of the three communities which represents the overall goal of this work.

2. DESCRIPTION OF LAKE

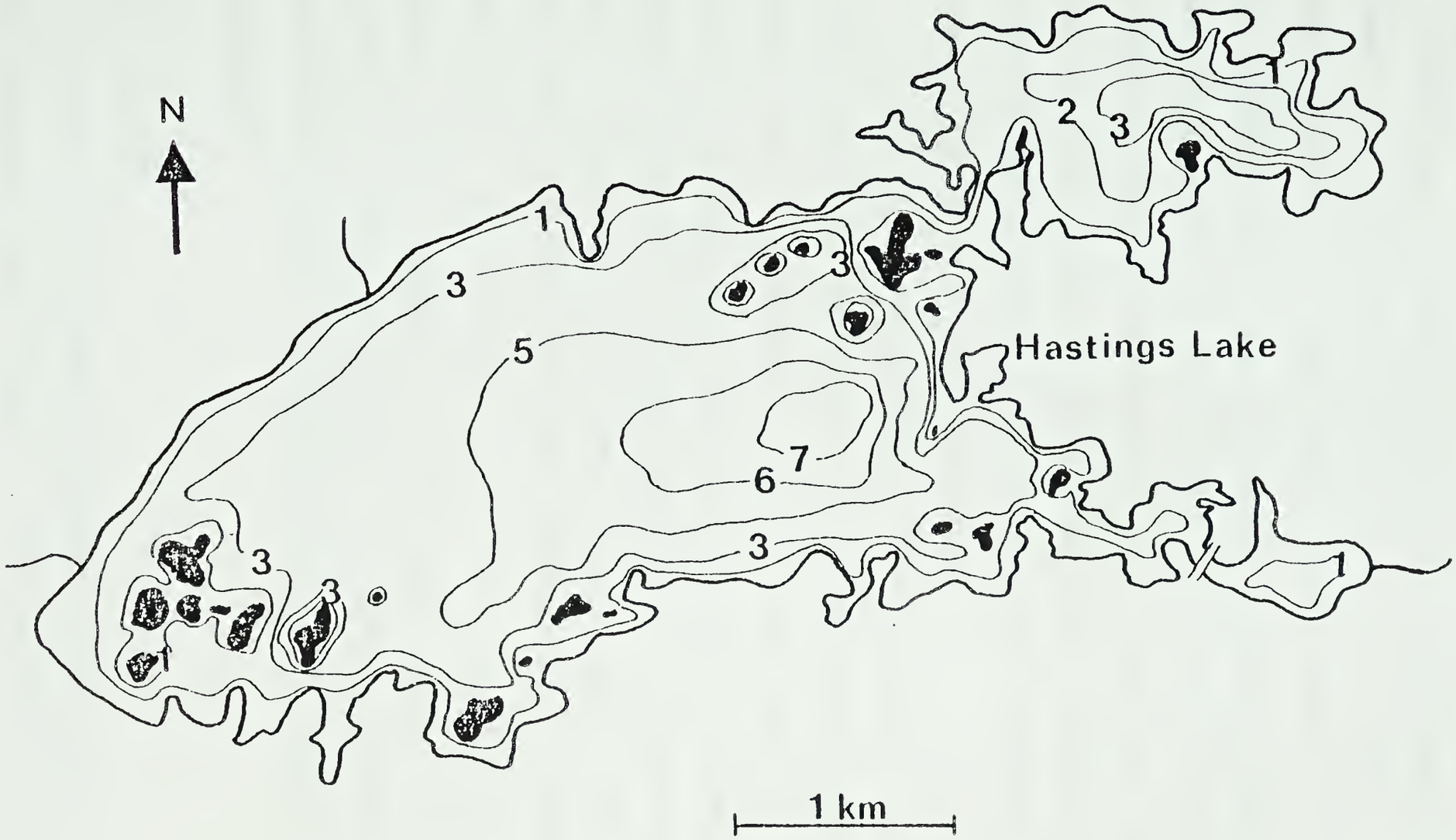
2.1. Location and Geology

Hastings Lake is located between longitudes 112°50' and 113°00' W, and latitudes 53°15' and 53°50' N in the Cooking Lake Moraine approximately 40 km ESE of Edmonton, Alberta (Figure 1). The bedrock geology is known as the Edmonton Formation and is composed of shales and sandstones (Bowser, et al. 1962). Sand, gravel, and silty glacial till mantled this during Wisconsin time; the surface till was deposited 9,000 to 11,000 years ago (Emerson 1977). The two basins of Hastings Lake were formed at this time as portions of the glacial ice sheet became detached and melted in situ forming several kettle lakes in the hummocky disintegration moraine (Bayrock and Hughes 1962, Forbes and Hickman 1981).

In the catchment area north of Hastings Lake, topographical relief is low with flat to slightly rolling hills, much of which has been cleared for pasture. To the south, a major east west moraine ridge is more forested (Schwartz and Gallup 1978, Forbes and Hickman 1981). Present day soils are poorly drained podzolic soils termed the Cooking Lake Loam (Bowser, et al. 1962).

The ground water table is at about 5 m depth following land relief, and surface runoff is generally from west to east across the watershed (Schwartz and Gallup 1978). Two intermittent inflows to the lake exist, one from the northwest, another from the west; an intermittent outflow is found on the southeast (Figure 1). No flow was observed during the course of this study.

Figure 1.
Bathymetric map of Hastings Lake.
Depth contours are drawn in meters.


N
Hastings Lake
1
2
3
5
6
7
1 km

2.2. Climate and Vegetation

The climate is northern continental with mild summers and cold winters. The average daily temperature is 2.3 °C; normal temperatures rarely go higher than 32 °C or lower than -40 °C. The area is moderately dry with precipitation decreasing eastward from the Rocky Mountains into the prairies. Average annual precipitation is 42.9 cm, about 70% of which occurs as rain and 30% of which occurs as snow. Weather patterns normally move from the northwest to the southeast as winds tend to be out of the northwest at an annual average velocity of 10 to 15 km/hr.

Much of the natural vegetation in the watershed has been cleared for pasture, especially to the northwest and southeast. Natural tree cover does remain virtually intact around the lake margin and to some extent toward the southwest and northeast. Populus balsamifera and Populus tremuloides are the major tree species, with small isolated stands of Picia glauca. These species are typical of the Boreal Parkland Transition zone of vegetation (Moss 1955). Aquatic vascular plants found in Hastings Lake include Scirpus validus, Phragmites australis, Typha latifolia, Myriophyllum exalbescens, Potamogeton vaginatus, Potamogeton richardsonii, Ceratophyllum demersum, Polygonum amphibia, Lemna trisulca, and Lemna minor.

2.3. Morphology

Hastings Lake is somewhat elliptical in shape with the long axis lying east to west (Figure 1). Thus, an effective fetch of 3.5

km is available for persistent northwest winds (Table 1). The lake is relatively shallow and has several small islands. A considerable potential for development of littoral communities exists as the shoreline development of 3.4 m indicates more than three times the shoreline available for colonization in a circular lake of the same area, and the mean depth of 2.5 m lies within the euphotic zone (3.2.1. Physico-chemical Parameters). Two basins joined by a shallow constriction are within the lake; the larger southwest basin comprises 81% and 92% of the total surface area and volume respectively.

Table 1. Morphometric features of Hastings Lake.

Elevation	735.8 m
Area	8.44 km
Volume	21.9 x 10 m
Length	6156.0 m
Maximum Width	2436.0 m
Maximum Depth	8.0 m
Mean Depth	2.5 m
Shoreline Length	35.5 km
Shoreline Development	3.40
Effective Fetch	3.5 km

3. PHYTOPLANKTON

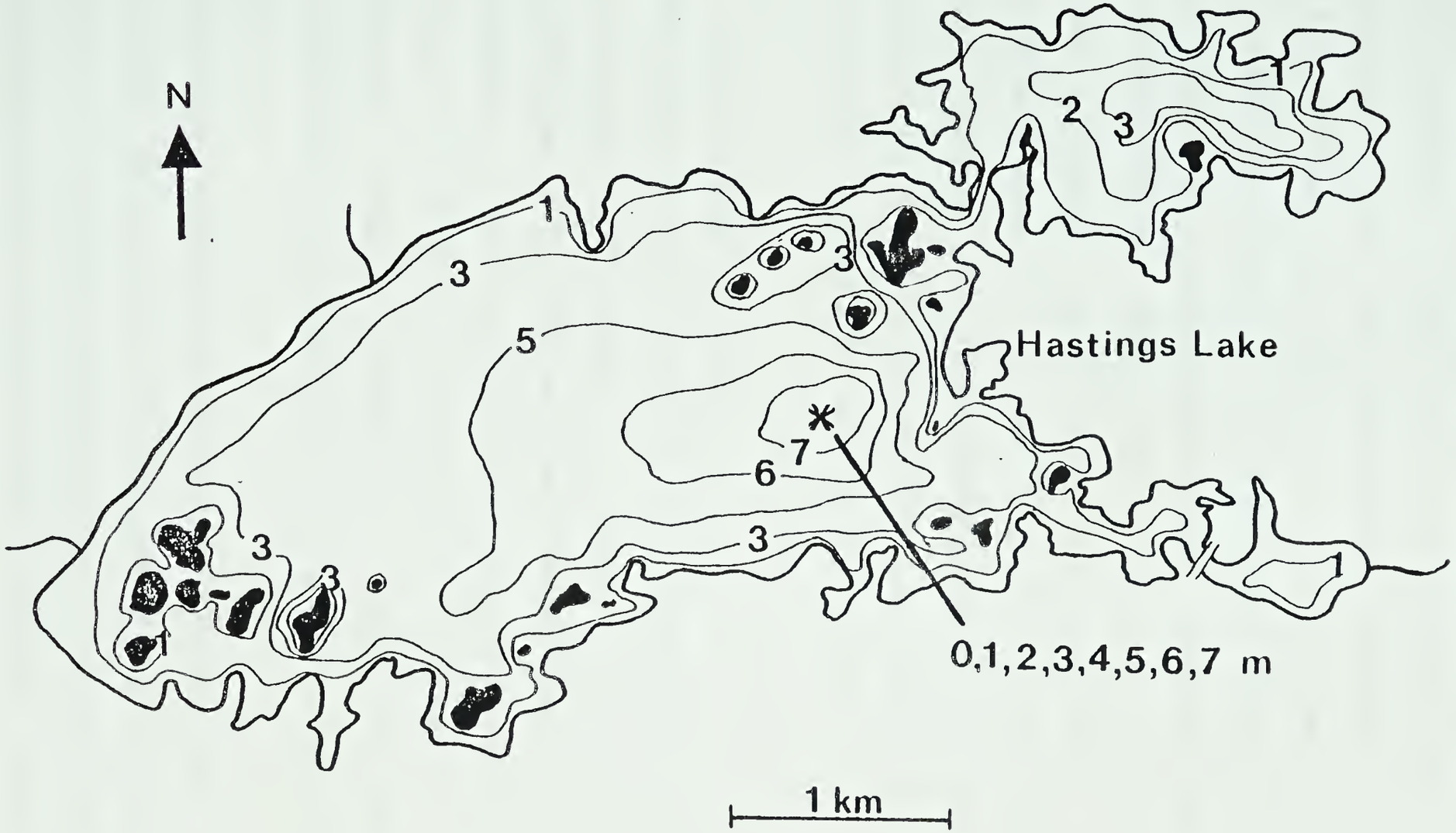
Traditionally, lake phytoplankton has been the focus of algal studies in ecology (Birge and Juday 1922, Pearsall 1932, Rodhe 1948, Ruttner 1952, Hutchinson 1967, Schindler 1974). However, the more classical aspects of lake turnover, stratification, and seasonal periodicity have not necessarily characterized prairie lakes in western North America (Hammer 1964, Waite and Duthie 1974, Haertel 1976). More specifically, the dimictic partitioning of lake periodicity into seasons is modified in the shallow, edaphically eutrophic prairie-parkland lakes of western Canada. That is, the seasons are empirically clothed in two distinct suits, each of which lasts approximately six months of the year; one is a period of persistent wind turbulence which interplays the rich supply of nutrients against the heavy demands of high algal standing crop; the other is a period of ice and snow cover which limits light (Bozniak and Kennedy 1968, Lin 1972, Hickman 1979a,b,c).

It was with this in mind that the phytoplankton of Hastings Lake was investigated. The aim of the phytoplankton part of this study was to characterize the community in terms of physico-chemical parameters, species, standing crop, and productivity. This would facilitate comparisons among the three major algal communities, namely the phytoplankton, epipelon, and epiphyton.

3.1. Methods

Samples were collected from a deep water station (Figure 2).

Figure 2.
Bathymetric map of Hastings Lake with
phytoplankton sampling station for
0, 1, 2, 3, 4, 5, 6, and 7 m depths indicated.


N
1
3
5
7
6
3
3
3
3
1
2
3
1
Hastings Lake
0,1,2,3,4,5,6,7 m
1 km

For the first two years of the study, samples were taken at 1 m intervals, 0 through 7 m. This was modified during the third year to one surface collection (0 m), two mid-depth collections (1, 2, 3, and/or 5 m), and one bottom collection (7 m). Samples were taken with a non-metallic, opaque 2.1 l Van Dorn sampler and kept in subdued light during subsequent manipulations. Sub-samples were taken for water chemistry analysis, species identification and enumeration, chlorophyll a analysis, and productivity studies. An attempt was made to sample once a week during the ice free period of 1974, once a fortnight during the ice free period of 1975, and once a month during the ice free period of 1976. When the lake was ice covered, sampling was done once per month when possible.

3.1.1. Physico-chemical Parameters

Mean monthly solar radiation data was obtained from Environment Canada data, Stoney Plain Station. C. F. Cassella actinographs were calibrated against a Kipp solarimeter and placed on shore at lake level to measure incident irradiance during productivity studies. The vertical distribution of light in the water column was determined with a submersible quantum sensor, Lambda Instruments Model LI-185, measuring photosynthetically available radiation, 400 to 700 nm.

Data on water temperature and oxygen concentrations were gathered with a Yellow Springs Instrument oxygen-temperature meter. Temperatures were expressed as degrees Celsius. Dissolved oxygen results were expressed as values of percent saturation calculated

from mg/l using a nomogram which incorporated oxygen, temperature, and altitude (Mortimer 1956).

The pH was measured with a Radiometer Model 29 pH meter immediately at a field lab, or within an hour at a university lab. Specific conductance was determined in the field during the first year of the study with a Hydrolab conductivity meter and similarly at a university lab when frozen samples were processed during the latter two years of the study.

For the portions of the study involving productivity, alkalinity was determined potentiometrically by titration to pH 4.6 with 0.1 N sulfuric acid into a 100 ml of fresh sample at the field laboratory (modified from American Public Health Association 1971). The meq bicarbonate was calculated by dividing alkalinity by 50 (Hutchinson 1957). Total inorganic carbon then was determined from pH and alkalinity following Saunders, et al. (1962).

For some of the water chemistry analysis sub-samples taken from the Van Dorn water bottle collections 0 to 7 m were placed in 1 liter polyethylene bottles. The water was then filtered and frozen for storage. Determinations for orthophosphate, nitrate, silica, sulfate, alkalinity, iron, and chloride were made on the thawed samples at a university laboratory utilizing American Public Health Association (1971) standard methods. Further chemical analyses were done on sub-samples from 0, 3, and 7 m, transferred in the field to glass jars, and processed by an Alberta government laboratory. There, potassium and sodium were determined by flame photometry, while calcium, carbonate, copper, magnesium, manganese, and zinc

were determined by atomic absorption spectometry. Data print outs were then provided.

3.1.2. Species

Sub-samples for species identification and enumeration were preserved with Lugol's Iodine Solution. Periodically, live samples were examined to check possible distortion of species by the preservative. A sample volume of 0.5 to 5.0 ml was sedimented in a settling chamber and scanned at 100X, 400X, and 1000X on a Wild M40 inverted microscope to identify species. Identifications were done utilizing Prescott (1961), Hustedt (1930), Patrick and Reimer (1966, 1975), Cleve-Euler (1951-1955), Desikachary (1959), and Bourrelly (1966, 1968, 1970).

Enumeration followed methods designed to ensure the $\pm$ 50% accuracy recommended for seasonal studies. At least 100 individuals were counted, theoretically yielding a $\pm$ 20% accuracy, and often more than 400 individuals were counted, yielding a theoretical accuracy of $\pm$ 10% (Lund, Kipling, and LeCren 1958, Kaatra and Harjula 1975). A coefficient of variation was calculated for actual cell counts total and for cell counts of dominant species selected to represent the seasons as follows: spring total cells 26%, spring dominant Stephanodiscus hantzschii 22%; summer total cells 39%, summer dominant Anabaena flos-aquae 60%, autumn total cells 33%, autumn dominant Chlamydomonas spp. 27%; winter total cells 60%, winter dominant Selenastrum minutum 48%.

Species diversity indices were determined using cell counts.

Species richness S was the total number of species. Species evenness E was calculated with a formula modified from Peilou (1966), $E = H/\log_{10}S$, where S is the number of species and H is as follows. Species diversity H was calculated using a formula modified from Shannon and Weaver (1963), $H = -\sum(n_i/N) \ln (n_i/N)$, where n_i is the cell count for each species and N is the total cell count for all species.

3.1.3. Chlorophyll *a*

Chlorophyll *a* determinations followed methods described by Moss (1967a,b). A 500 to 1500 ml sample of lake phytoplankton was filtered through Whatman GF/C. The filter pad with filtered algae was then added to 10 ml of 90% acetone buffered with anhydrous magnesium carbonate and the preparation was routinely macerated. The pigments were extracted in the dark at freezer temperatures for 24 hours. Then the sample was centrifuged five to ten minutes at 5,000 rpm to sediment filter fibers, magnesium carbonate, and particulate cell matter. A spectrophotometric analysis of the sample in its non-acidified and then in its acidified state corrected for naturally occurring degradation to pheophytin *a* and yielded active chlorophyll *a* expressed on a per volume basis.

The coefficients of variation calculated for the total method on samples selected from each of the four seasons were as follows: for the spring 4%, for the summer 13%, for the autumn 7%, and for the winter 15%.

3.1.4. Productivity

Primary productivity was estimated the last 17 months of the study using carbon-14 methods. In the field, carbon-14 ($NaHC^{14}O_3$) was added to phytoplankton samples in 125 ml glass incubation bottles. Two light bottles and one dark bottle for each collection depth 0 to 7 m were suspended from a float system and incubated *in situ* for 4 hours from 1030 to 1430 hours. At the end of the incubation period, carbon fixation was terminated by the addition of formaldehyde.

In the laboratory, samples were acidified and bubbled to drive off any inorganic carbon-14 (Schindler, Schmidt, and Reid 1972). Sub-samples were then combined with Aquasol scintillation fluor and the activity determined using a Nuclear-Chicago Mark I Liquid Scintillation Computer Model 6860. Values were then corrected for quenching and calculated on an mg carbon/hr/m^3 basis.

The coefficients of variation calculated for the total method on samples selected from each of the four seasons were as follows: spring 8%, summer 16%, autumn 6%, and winter 10%.

3.1.5. Cross Incubation Studies

In cross incubation studies, productivity samples were collected at the top of the euphotic zone (0 m), near the bottom of the euphotic zone (1, 2, or 3 m), near the top of the aphotic zone (3 or 5 m), and at the bottom of the aphotic zone (7 m). This facilitated comparisons of possible active/senescent and sun/shade populations through the manipulation of incubation depths. That is,

productivity samples from each collection depth were incubated at that respective depth as well as every other collection depth, creating a matrix of cross incubations.

3.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

Values for the photosynthetic index, photosynthetic efficiency, and productivity efficiency were defined in a manner analogous to concepts utilized in other studies. The photosynthetic index was determined by productivity per standing crop (Fogg 1963), i.e. mg carbon/hr/m^3 ÷ mg chlorophyll _a_/m^3. The photosynthetic efficiency was productivity per irradiance (Tilzer, _et al_. 1975), i.e. mg carbon/hr/m^3 ÷ cal/hr/cm^2. The productivity efficiency incorporated standing crop and irradiance (Eloranta 1976), i.e. mg carbon/hr/m^3 ÷ (mg chlorophyll _a_/m^3 x cal/hr/cm^2). These functions were not necessarily calculated as were those of other studies. The intent was a direct comparison with other communities investigated in this study and an indirect comparison with spatial and temporal patterns reported in other studies.

3.2. Results

3.2.1. Physico-chemical Parameters

Global insolation at this northerly latitude showed marked monthly increases in cal/cm^2/day from January through June and likewise marked monthly decreases from July to December (Table 2). Monthly averages ranged from less than 50 cal/cm^2/day in winter to

Table 2. Physico-chemical parameters. Ion concentrations are in mg/l.

Mo./ Yr.	Irradiance $cal/cm^2/day$	m depth 1% Ph.A.R.	CO_3	Cl	Mg	K	Na	Fe	Mn	Cu	Zn
05/74	510	2.7	10	6	39	32	92	.01	.02	.01	.01
06/74	625	2.1	14	9	43	24	82	.02	.02	.01	.02
07/74	590	1.7	32	11	45	22	81	.05	.03	.03	.16
08/74	460	1.4	33	8	43	19	80	.04	.03	.01	.03
09/74	310	1.3	18	7	43	24	86	.05	.02	.01	.02
10/74	220	2.0	14	8	42	26	78	.02	.01	.01	.02
11/74	110	-	<5	8	44	30	87	.03	-	-	-
12/74	50	-	6	7	45	32	90	.06	-	-	.19
01/75	80	1.8	6	4	42	29	98	.07	.01	.01	-
02/75	190	1.8	-	7	51	29	99	.06	-	-	-
03/75	340	0.5	-	21	23	34	110	.09	-	-	.10
04/75	420	-	-	-	-	-	-	-	-	-	-
05/75	510	1.8	21	9	42	29	72	.04	.02	.01	-
06/75	560	3.2	-	9	40	28	94	.03	.03	+++	-
07/75	500	1.3	19	6	45	24	80	.03	.05	+++	-
08/75	415	0.8	27	7	44	26	82	.03	.06	+++	-
09/75	350	1.7	-	8	43	29	88	.05	.02	.01	-
10/75	182	2.5	<5	9	42	28	85	.02	.01	.01	-
11/75	107	-	-	-	-	-	-	-	-	-	-
12/75	65	-	-	-	-	-	-	.02	-	-	-
01/76	75	1.5	-	8	51	25	102	.03	.06	.01	-
02/76	160	1.0	7	13	55	31	103	-	.09	.01	-
03/76	360	0.5	-	9	60	35	102	.04	-	-	-
04/76	440	0.5	-	8	51	26	108	.03	-	+++	-

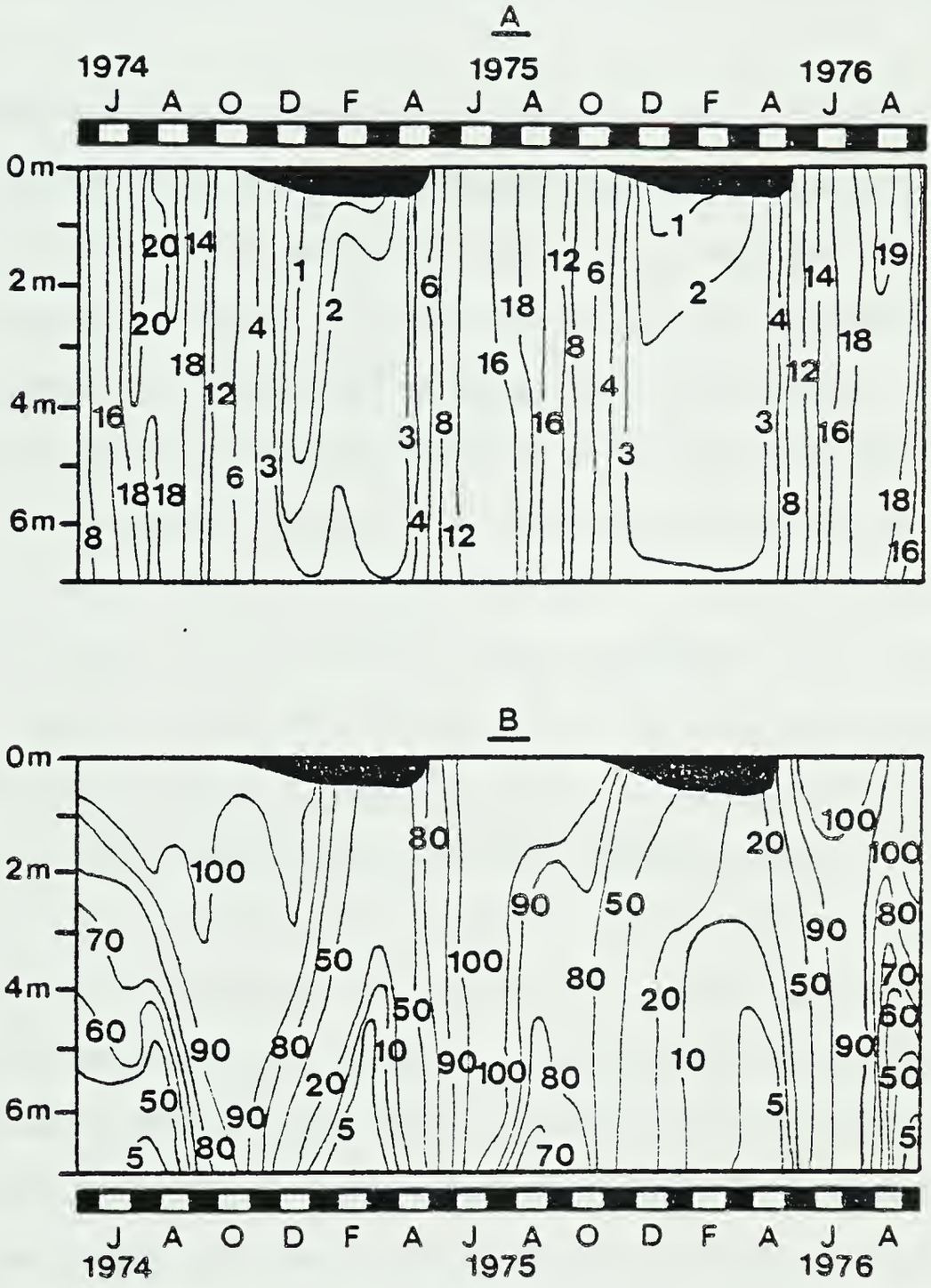
more than 600 cal/cm²/day in late spring/early summer.

The penetration of incident irradiance into the pelagial zone of Hastings Lake was of special note. The sharp attenuation of light restricted the euphotic zone, as defined by the 1% light level. The mean 1% level was 2 m, range 0.5 to 3.5 m. On a seasonal basis, light penetration was greatest in spring and autumn, and least under phytoplankton shading in summer, and ice and snow in winter (Table 2).

Water temperatures are presented in a time-depth diagram (Figure 3a). After spring ice break-up and turnover during the first week of May 1974, homoiothermic conditions were established because of the lake's low surface to volume ratio, and the lake's exposure to prevailing NNW winds. The absence of thermal stratification persisted through the spring, summer, and autumn of 1974. Twice during the summer exceptions were recorded. First on 24 June, there was a 1.5 °C difference in temperature between 4 and 5 m depths, then on 22 July, there was a 1 °C difference between 3 and 4 m. The maximum difference in 0 and 7 m temperatures for the ice free May to November 1974 period also occurred on those dates; a 2.5 °C difference was recorded on 24 June, with a 2 °C appearing after 2 to 3 days of calm sunny weather and disappearing with the onset of the usual wind turbulence. From mid-June to mid-August, surface water temperatures remained stable within a 18 to 21 °C range. Then, September through November, lake water temperatures quickly decreased.

Ice formed the second week of November and inverse

Figure 3.
Time-depth diagram of lake water temperature in °C (A) and time-depth diagram of percent saturation oxygen (B) for the phytoplankton.


A
1974
1975
1976
J A O D F A J A O D F A J A
0m
2m
4m
6m
B
0m
2m
4m
6m
J A O D F A J A O D F A J A
1974
1975
1976

stratification began. December 1974 through March 1975, water temperatures just under the ice were near 0 °C; temperatures at 7 m were near 4 °C. There were slight fluctuations. Especially noteworthy were irregular increases just below the ice and at the 7 m depth.

Daylength and air temperature increased markedly in April 1975. With increasing daylengths and air temperature and the spring ice break-up occurring the first week of May, a cycle very similar to the previous year's began. Homoiothermic profiles existed through spring, summer, and autumn with no exceptions. The summer temperatures were stable within the 15 to 20 °C range from late June through late September. The maximum difference in temperature between 0 m and 7 m was 2.5 °C on 6 September. The lake cooled quickly in October, and by the first week in November it was ice covered. Again, inverse stratification occurred under winter ice with temperatures near 0 °C just underneath the ice surface and near 4 °C at 7 m. This temperature regime was relatively stable throughout the ice covered period, November 1975 through April 1976. A warming trend began under ice in April 1976, and by late in the month ice break-up occurred, almost two weeks earlier than spring ice break-up in 1975. No persistent temperature stratification was recorded for the spring, summer, or autumn of 1976. On 8 August a short-lived profile was found. Differences of 1 °C between 1 and 2 m, 2 and 3 m, and 6 and 7 m were recorded. On this date too, the maximum temperature difference between 0 m and 7 m occurred, a range of 3 °C. Temperatures between mid-June and mid-September were in

the 15 to 19 °C range. But by October, the temperatures had decreased greatly.

A time-depth diagram of percent oxygen saturation is presented (Figure 3b). Immediately after spring ice break-up in May of 1974, a clinograde oxygen depth profile developed. This marked stratification continued through the spring and into the summer with oxygen values greater than 100% common in the euphotic zone 0 to 2 m and less than 10% in the aphotic zone just above the lake bottom. The stratification broke down in mid-August. Values exceeding 80% were recorded throughout the water column in late August, September, October, and November. Levels in excess of 100% continued to be present in the upper 2 m. Under newly formed ice in November, supersaturation extended to a depth of 5 m.

Under ice cover from December 1974 through March 1975, oxygen levels just under the ice steadily decreased to a low of 38%. During this period, saturation values below 10% were found near the lake bottom, and in March, the entire region 4 m to lake bottom was less than 10%. Oxygen levels began to increase in early April still under ice cover. With ice break-up during the first week of May 1975, there were uniformly high percent saturation values for the entire water column and this condition continued through the spring, summer, and autumn with no stratification evident. Levels in excess of 100% were maintained throughout the water column during June and July, and in the top 2 to 3 m during August, September, and October. Then the percent saturation began to decrease rapidly toward the end of October and into November as ice formed.

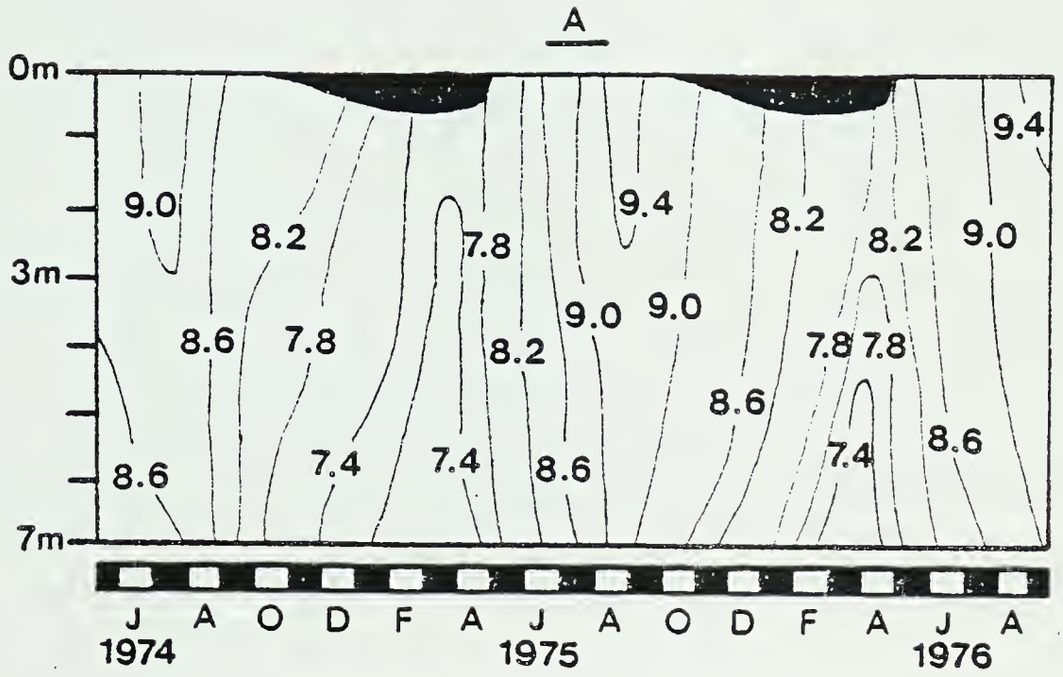
A more gradual drop then followed in December 1975 through March 1976, when an 11% saturation value was found just beneath the ice. Oxygen levels less than 10% were first noted in December 1975 at the lower depths, and by March 1976, readings below 10% existed from one-half meter below the ice down to the lake bottom. An increase of surface values occurred under ice in April 1976, much as in April 1975.

After ice break-up during the last week of April 1976, isopleths indicated high uniform saturation, and values in excess of 100% occurred 0 to 1 m. This continued through May, June, and July. A period of stratification began in August with levels 90 to 100% at the surface to less than 30% at 7 m. This clinograde stratification persisted through September and October when the final data was collected.

A tabulation of water chemistry data is presented as monthly means of the 0 to 7 m water column for carbonate (CO_3), chloride (Cl), magnesium (Mg), potassium (K), iron (Fe), manganese (Mn), copper (Cu), and zinc (Zn) to facilitate comparisons over a variable sampling schedule May 1974 through April 1976 (Table 2). The pH, conductivity, calcium (Ca), bicarbonate (HCO_3), sulfate (SO_4), silica (SiO_2), nitrate (NO_3), and orthophosphate (PO_4) are presented as time-depth diagrams because of the potential for dynamic spatial and temporal relationships with lake biota (Figure 4, Figure 5, Figure 6, Figure 7).

The pH showed a general decrease with depth; the maximum change in values from 0 to 7 m approached 1.0 and occurred during summer

Figure 4.
Time-depth diagram of pH (A) and time-depth diagram of conductivity expressed as micromhos/cm (B) for the phytoplankton.


A
0m
3m
7m
9.0
8.2
7.8
9.4
8.2
8.2
9.0
9.0
9.0
8.6
7.8
8.2
7.8
7.8
8.6
8.6
7.4
7.4
8.6
7.4
8.6
J A O D F A J A O D F A J A
1974
1975
1976

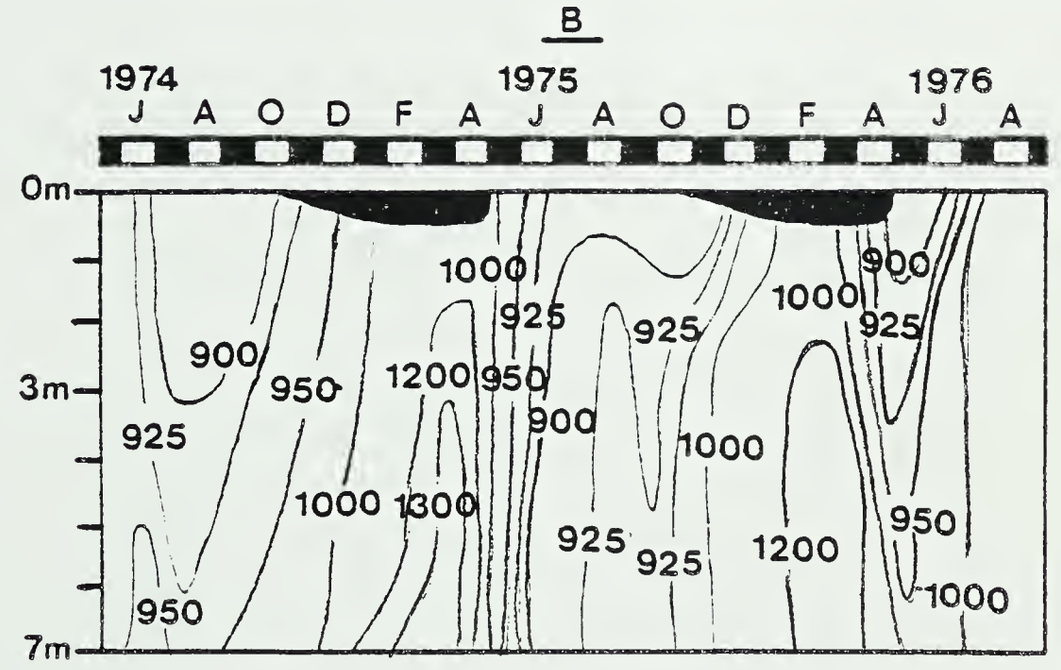
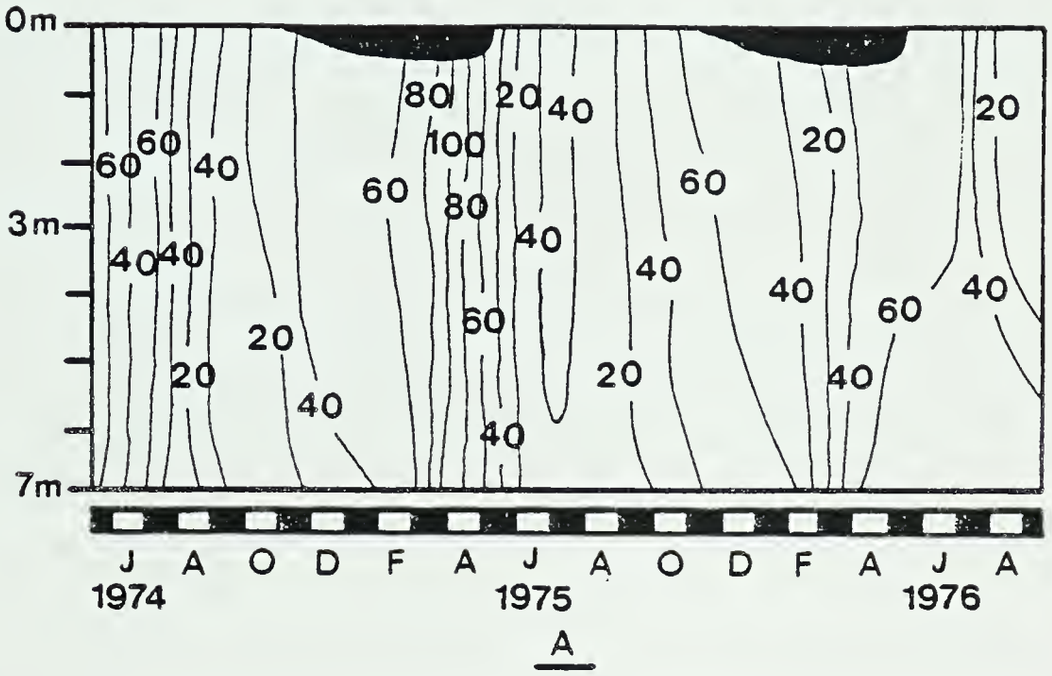
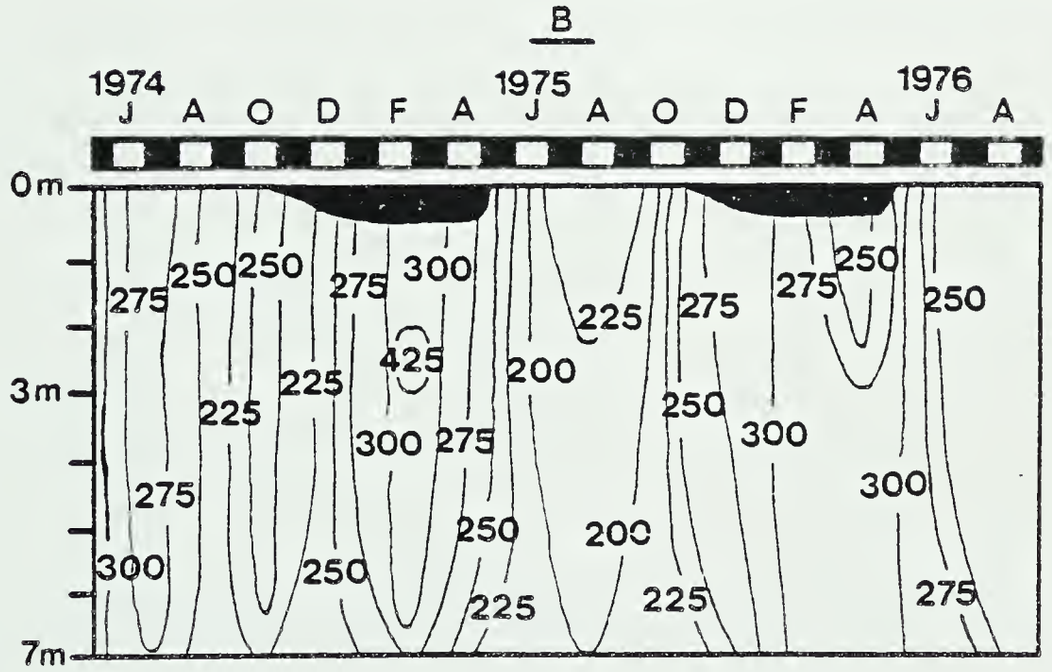

B
1974
1975
1976
J A O D F A J A O D F A J A
0m
3m
7m
1000
925
900
1000
900
925
925
900
950
1200
950
925
900
1000
1000
1300
925
925
1200
950
950
1000

Figure 5.
Time-depth diagram of mg calcium/l (A) and
time-depth diagram of mg sulfate/l (B)
for the phytoplankton.

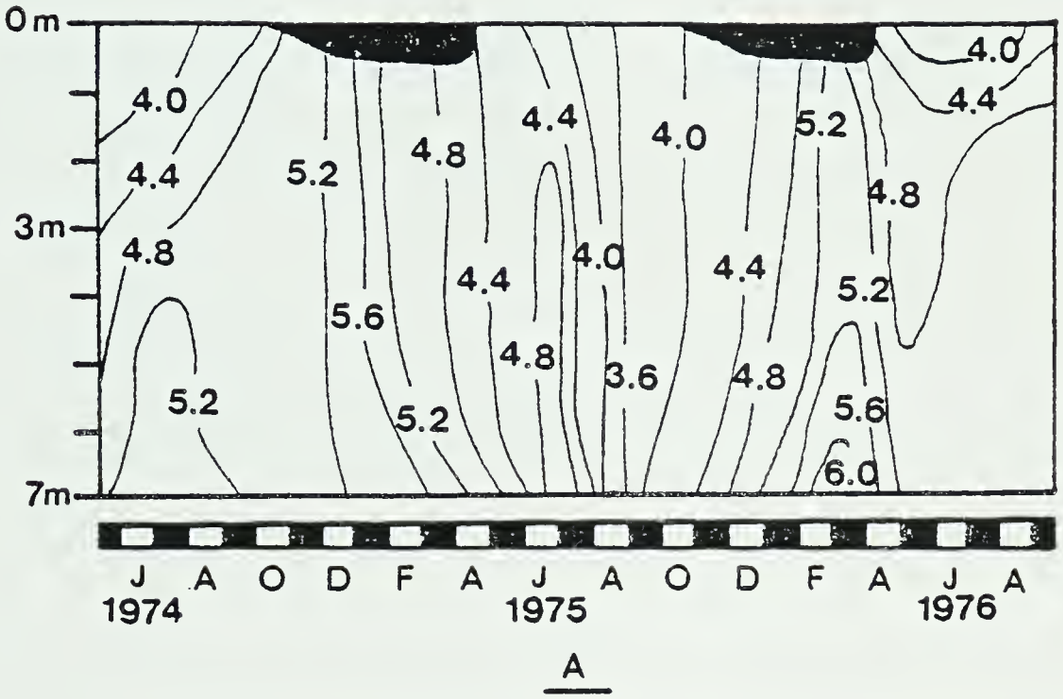

0m
3m
7m
80
20
40
60
100
60
60
40
60
80
40
40
40
40
60
20
20
40
20
20
40
40
60
40
20
40
J A O D F A J A O D F A J A
1974
1975
1976

A

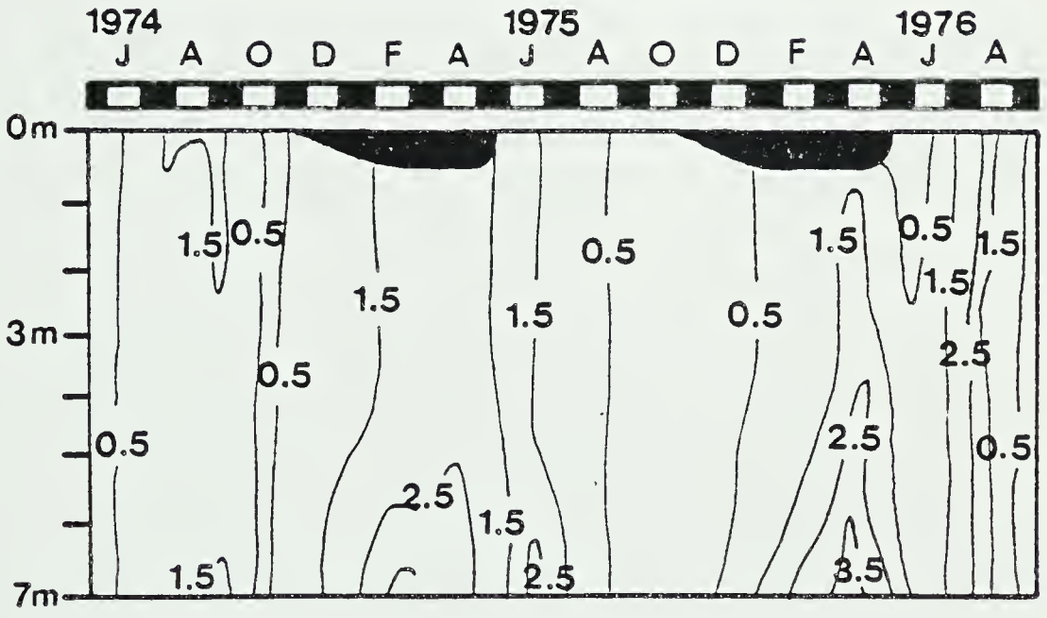

1974
1975
1976
J A O D F A J A O D F A J A
0m
3m
7m
275
250
250
275
300
225
275
275
250
425
200
225
225
250
300
275
300
275
250
200
300
300
250
225
225
275

B

Figure 6.
Time-depth diagram of meq bicarbonate (A) and
time-depth diagram of mg silica/l (B)
for the phytoplankton.

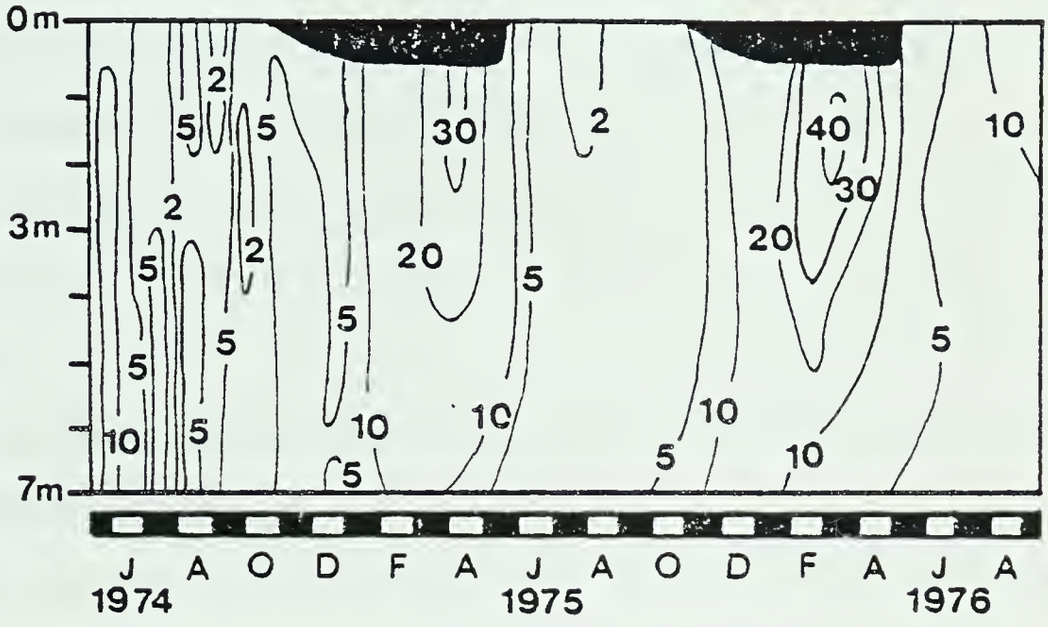

0m
3m
7m
4.0
4.4
4.8
5.2
5.6
6.0
3.6
J A O D F A J A O D F A J A
1974
1975
1976

A

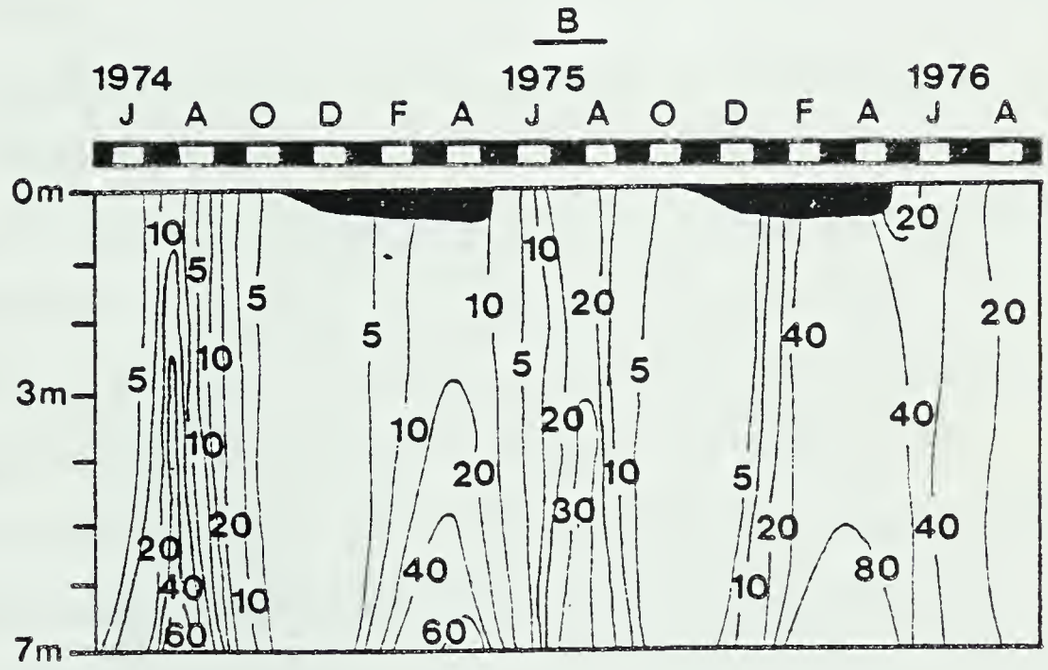

1974
1975
1976
J A O D F A J A O D F A J A
0m
3m
7m
0.5
1.5
2.5
3.5

B

Figure 7.
Time-depth diagram of mg nitrate/l x 10^2 (A)
and time-depth diagram of mg orthophosphate/l
x 10^2 (B) for the phytoplankton.


0m
3m
7m
J A O D F A J A O D F A J A
1974
1975
1976

A


1974
1975
1976
J A O D F A J A O D F A J A
0m
3m
7m

B

and winter (Figure 4a). Seasonal fluctuations of the monthly means were relatively steady with the highest values in summer and the lowest in winter (Table 2). The range from 7.3 to 9.3 extended over a mean of 8.2 $\pm$ 0.5 during the two year period.

Specific conductance, expressed as micromhos/cm, is one representation of major ions in a lake. Conductivity units increased with depth; the maximum difference between 0 and 7 m was 220 micromhos/cm noted in February 1975 (Figure 4b). Seasonal values moved gradually from summer minima to winter maxima (Table 2). The two year mean was 984 $\pm$ 115 micromhos/cm with a range of 833 to 1263 micromhos/cm.

The major ions in Hastings included the four cations sodium > calcium > magnesium > potassium along with the four anions sulfate > bicarbonate > carbonate > chloride. Hastings then is a sodium sulfate lake, as are the other prairie-parkland lakes in the Cooking Lake Moraine (Potter 1977). The importance of bicarbonate and calciums is also evident.

Each of the four cations showed highest concentrations during winter (Table 2). The mean sodium level was 90 $\pm$ 11 mg/l over a range of 78 to 110 mg/l. Calcium was the only cation presented as a time-depth diagram, as there was a potential for spatial and temporal associations with lake biota (Figure 5a). However, data indicated an equal distribution of calcium with depth was most common. Seasonal fluctuations were more irregular than those of the other cations with a mean of 44 $\pm$ 18 mg/l and a range of 19 to 101 mg/l. Magnesium and potassium levels were similar to calcium but

not as erratic, the respective means being 44 ± 7 mg/l and 28 ± 4 mg/l and the respective ranges being 23 to 63 mg/l and 19 to 35 mg/l.

The anion sulfate showed a slight tendency to decrease with depth, but exceptions did occur, especially during February, March, and April 1976 (Figure 5b). Seasonal values varied, but summer levels tended to be low and winter levels high (Table 2). Concentrations averaged 253 ± 46 mg/l and ranged from 132 to 338 mg/l.

In the pH range of Hastings, bicarbonate is the major source of carbon for photosynthesis. Its vertical distribution was similar to that of conductivity as meq values tended to increase with depth; the maximum difference between 0 and 7 m was 1.7 meq in July 1974 (Figure 6a). Monthly means of bicarbonate were somewhat variable, but generally summer minima and winter maxima occurred (Table 2).

A minor carbon source existed as the anion carbonate. It was the only major ion to have summer maxima and winter minima (Table 2). The average was 15 ± 10 mg/l and the range was 5 to 33 mg/l. The remaining anion chloride both increased and decreased rapidly around mid-winter maxima; concentrations averaged 9 ± 3 mg/l and showed a range of 4 to 21 mg/l.

Minor ions by mass, but of considerable importance to the biota as micronutrients, are iron, manganese, copper, and zinc. The mean iron concentration was 0.04 ± 0.02 mg/l over a range of 0.01 to 0.09 mg/l. Although month to month changes were erratic and data during the winter of 1975/1976 was sparse, the highest values occurred in

winter (Table 2). Manganese data and limited zinc data show winter and summer peaks over respective ranges of 0.01 to 0.09 mg/l and 0.01 to 0.19 mg/l with respective averages of 0.03 $\pm$ 0.02 mg/l and 0.07 $\pm$ 0.07 mg/l (Table 2). Copper showed only a summer peak over a range of < 0.01 to 0.03 with a mean of 0.009 $\pm$ 0.006 mg/l (Table 2).

Silica is a nutrient which is present in fresh water at relatively low concentrations, but which is a major nutrient. Measures of silica concentrations with depth showed distinct profiles. A slight depletion was shown in surface waters in spring of 1975 and 1976. The most distinct distributions were found during winter under ice; for example, in March of 1975, 2.05 mg/l levels at 0 m increased to 3.80 mg/l at 7 m, and in March of 1976, 1.20 mg/l levels at 0 m increased to 3.30 mg/l at 7 m (Figure 6b). The seasonal fluctuations of monthly means in 1974 indicated spring and autumn low concentrations less than, or equal to, 0.50 mg/l. A summer peak near 1.00 mg/l occurred. During the winter of 1974/1975, annual maxima were more than 2.00 mg/l. No spring lows, nor summer highs, were noted in 1975. A steady decline from high winter concentrations continued through spring and summer into autumn lows. Levels below 0.50 mg/l were recorded in August, September, October, and November. The 1975/1976 winter maxima quickly followed, again with values over 2.00 mg/l. In 1976 a spring low near 0.50 mg/l and a summer high greater than 2.00 mg/l occurred before the collection of samples for chemistry ceased. Silica averaged 1.18 $\pm$ 0.70 mg/l over a range of 0.30 to 2.30 mg/l.

Likewise, nitrate does not account for a great deal of mass in

freshwaters, but it does function as a major nutrient source. The spatial distribution of nitrate was interesting in Hastings. During the ice free seasons, a slight increase with depth was evident, especially during 1974 (Figure 7a). However, in the latter half of the winter under ice cover, a marked decrease with depth occurred; for example, in March of 1975 at 0 m and 7 m, levels were 0.32 and 0.04 mg/l, respectively. Data showed low summer concentrations and high winter concentrations. Values ranged from 0.04 to 0.24 mg/l and averaged 0.10 $\pm$ 0.06 mg/l.

Of the three major nutrients, phosphate is considered the least abundant in nature and the most likely to limit phytoplankton metabolism. Orthophosphate in Hastings showed increases with depth during summer and winter periods, and an even distribution with depth in spring and autumn (Figure 7b). Maximum differences between 0 and 7 m occurred late in June of 1974 with values of 0.14 and 0.71 mg/l, respectively, then again in March of 1975 with values of 0.29 and 1.02 mg/l. Data indicated a peak in summer and an annual maximum in winter. Concentrations ranged from 0.03 mg/l in spring and autumn to 0.76 mg/l in winter. The average over the two year period was 0.20 $\pm$ 0.23 mg/l.

3.2.2. Species

Of the 124 species identified from the phytoplankton, 19 formed dominant populations, i.e. 20% of the respective total cell counts (Table 3). From the dominant populations three species were chosen to illustrate representative spatial distributions depth by depth

Table 3. Dominant species found in the phytoplankton.

CYANOPHYTA:

- *Anabaena circinalis* Rabenhorst
- *Anabaena flos-aquae* (Lyng.) deBreb.
- *Aphanizomenon flos-aquae* (L.) Ralfs
- *Coelosphaerium naegelianum* Unger
- *Gomphosphaeria lacustris* var. *compacta* Lemm.
- *Lyngbya lagerheimii* (Moebius) Gomont
- *Merismopedia tenuissima* Lemm.
- *Microcystis aeruginosa* (Kutz.) Elenkin
- *Oscillatoria subbrevis* Schmidle

CHLOROPHYTA:

- *Botryococcus sudeticus* Lemm.
- *Chlamydomonas* spp. Ehr.
- *Chorella vulgaris* Beyer
- *Crucigenia quadrata* Morren
- *Gonium sociale* (Duj.) Warming
- *Kirchneriella contorta* (Schmidle) Bohlin
- *Pandorina morum* (Muell.) Bory
- *Selenastrum minutum* (Naeg.) Collins

BACILLARIOPHYTA:

- *Stephanodiscus hantzschii* Grun.

CRYPTOPHYTA:

- *Rhodomonas minuta* Skuja

(Figure 8, Figure 9, Figure 10). All dominants have been presented on a temporal basis as graphs of the means for all collection depths (Figure 11).

During the ice free May to November period, the vertical distribution of dominant species was generally irregular to even. However, occasional sampling dates coincided with short periods of calm weather, and the potential for surface concentrations of vacuolated cyanophycean species was expressed. Anabaena circinalis, Anabaena flos-aquae, and Aphanizomenon flos-aquae all exhibited this type of distribution. A graph of Anabaena circinalis illustrates the concentration of standing crop in the upper 2 m of the water column (Figure 8). From November through April under winter ice, the flagellates Chlamydomonas spp., Gonium sociale, and Rhodomonas minuta also maintained their largest populations in the upper 2 m. A graph of Rhodomonas minuta represents this type of distribution; however, during the ice free period, the irregular to even pattern was shown by this species also (Figure 9).

All the remaining dominants showed the more typical irregular to even distribution year round. Such profiles were characteristic of the bacillariophyte Stephanodiscus hantzschii and the cyanophytes Gomphosphaeria lacustris var. compacta, Lyngbya lagerheimii, and Merismopedia tenuissima, including even the vacuolated species Coelosphaerium naegelianum, Microcystis aeruginosa, and Oscillatoria subbrevis. The chlorophytes Botryococcus sudeticus, Chlorella vulgaris, Crucigenia quadrata, Kirchneriella contorta, Selenastrum minutum, and even the flagellate Pandorina morum also showed this

Figure 8.
Seasonal distribution of
Anabaena circinalis
depth by depth for the phytoplankton.

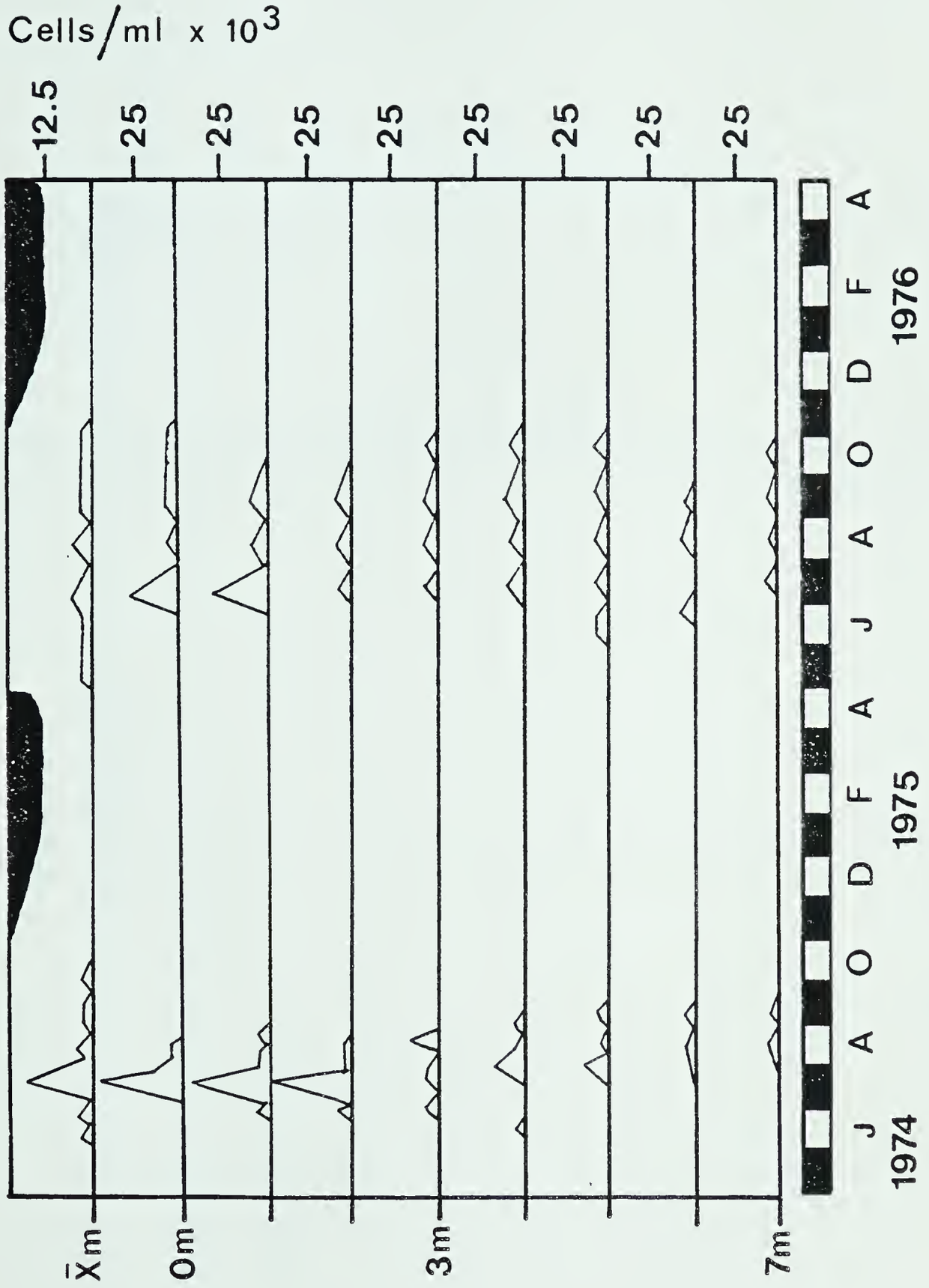

Cells/ml x 10³
12.5
25
25
25
25
25
25
25
X̄m
0m
3m
7m
J A O D F A J A O D F A
1974
1975
1976

Figure 9.
Seasonal distribution of
Rhodomonas minuta
depth by depth for the phytoplankton.

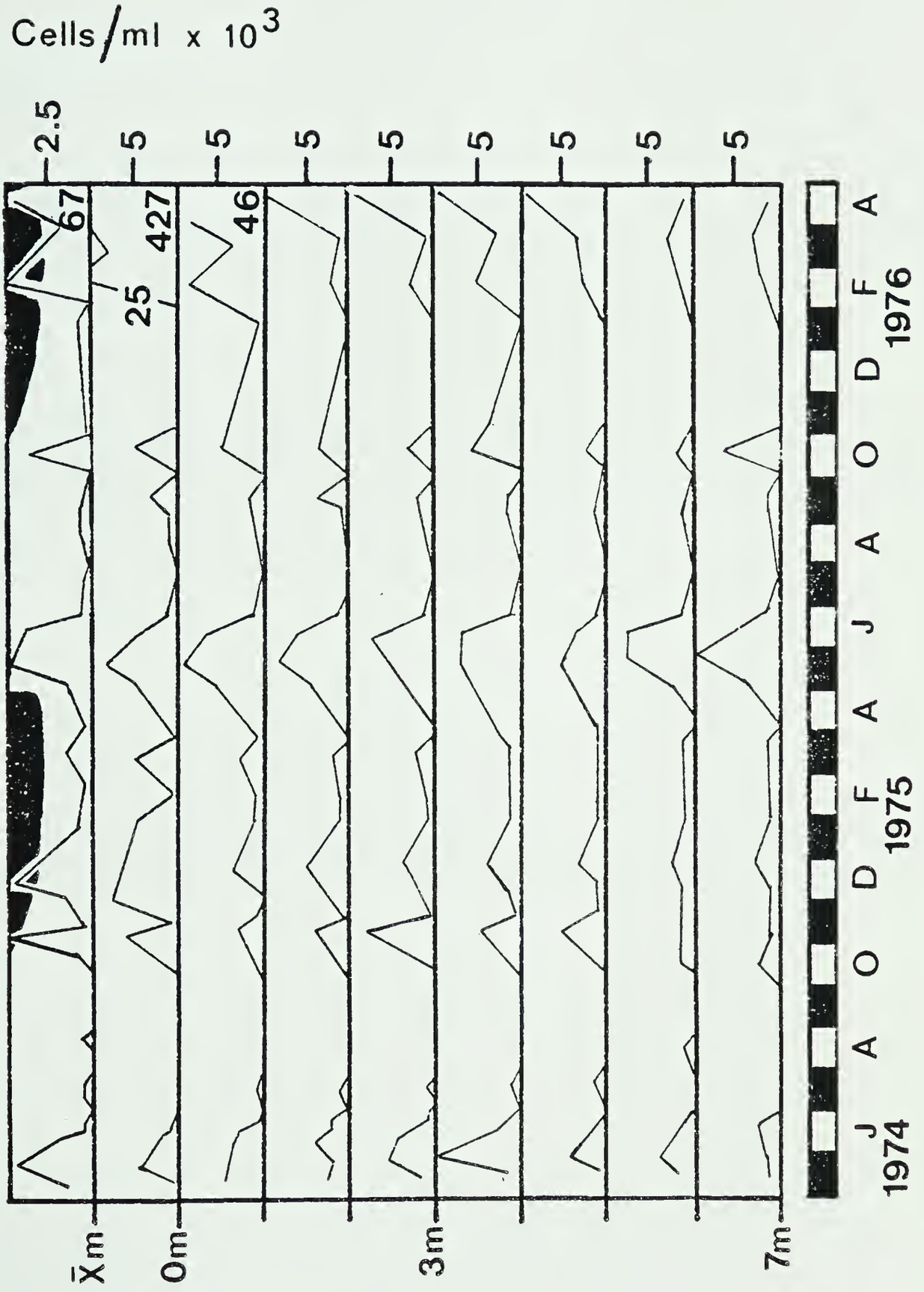

Cells/ml x 10^3
2.5
5
5
5
5
5
5
5
67
427
46
25
$\bar{X}$m
0m
3m
7m
J A O D J F A J A O D J F A
1974
1975
1976

Figure 10.
Seasonal distribution of
Selenastrum minutum
depth by depth for the phytoplankton.

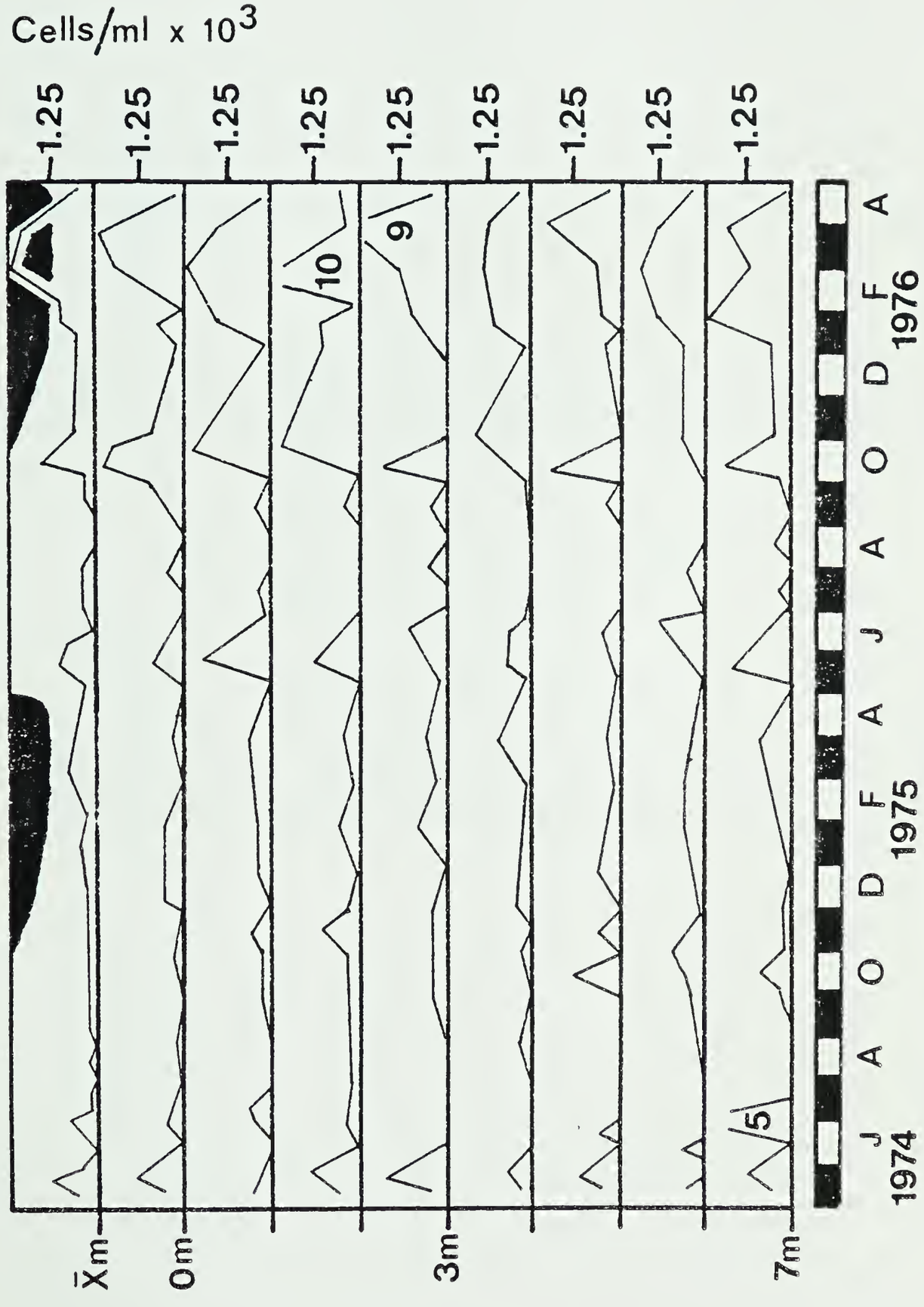

Cells/ml x 10^3
1.25
1.25
1.25
1.25
1.25
1.25
1.25
1.25
10
9
5
$\bar{X}$m
0m
3m
7m
J
1974
A
O
D
F
1975
A
J
A
O
D
F
1976
A

Figure 11.
Seasonal distributions of
A. *Merismopedia tenuissima*,
B. *Anabaena flos-aquae*,
C. *Aphanizomenon flos-aquae*,
D. *Microcystis aeruginosa*,
E. *Coelosphaerium naegelianum*,
F. *Oscillatoria subbrevis*,
G. *Gomphosphaeria lacustris* var. *compacta*,
H. *Stephanodiscus hantzschii*,
I. *Crucigenia quadrata*,
J. *Botryococcus sudeticus*,
K. *Chlorella vulgaris*,
L. *Kirchneriella contorta*,
M. *Chlamydomonas* spp.,
N. *Gonium sociale*, and
O. *Pandorina morum*
for the phytoplankton.

Cells/ml x 10³
Cells/ml x 10³
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
5
20
2
5
2
2
1
1
60
13
43
241
127
302
265
50
11
5
6
3
6
9
J
1974
A
O
D
F
1975
A
J
A
O
D
F
1976
A

typical vertical profile. For example, Selenastrum minutum counts during the first half of May 1974 were similar for 0 through 7 m, but in the latter half of the month counts were higher at 0, 2, 3, 5, and 7 m and lower at 1, 4, and 6 m (Figure 10). This more general type vertical distribution was shown by 13 of the 19 dominant algae.

For the most part, dominant species peaked temporally within specific seasonal boundaries, and did not maintain major populations through marked physico-chemical changes in the environment. Species then could be characterized as spring/autumn, summer, or winter populations. Dominance has been determined relative to the other populations within the community; so indeed, an active population may be at increasing, high, decreasing, or low counts and be dominant dependent upon the current status of community standing crop fluctuations.

Seven of the eight chlorophycean dominants were spring and/or autumn species (Figure 11). Crucigenia quadrata maxima occurred in June, and the species was a dominant in June of 1974. Chlorella vulgaris, Kirchneriella contorta, Selenastrum minutum, and the flagellate Chlamydomonas spp. exhibited spring/autumn peaks. But, it was under winter ice when their seasonal cell counts were low, that all four of these species were dominants. Dominant populations did occur in addition for Chlorella vulgaris during autumn of 1974, and for Chlamydomonas spp. during spring of 1975. The flagellates Gonium sociale and Pandorina morum each displayed spring/autumn peaks and had large winter populations as well. For both species,

it was the large winter populations that were dominants in the community. The one remaining chlorophycean dominant Botryococcus sudeticus showed a summer peak in 1974 and was a dominant at that time.

Among the cyanophycean dominants (Figure 11), only Gomphosphaeria lacustris var. compacta showed spring/autumn peaks; it was a dominant in a 1975 autumn peak. It also peaked during winter 1974/1975, being dominant once when counts were high, and once when counts were low. Merismopedia tenuissima numbers were high in spring and summer; in 1974 counts continued to increase spring through summer, but in 1975 high spring numbers decreased before increasing again to high summer counts. It was a dominant when large spring/summer populations existed. Anabaena circinalis, Anabaena flos-aquae, Aphanizomenon flos-aquae, Microcystis aeruginosa, and Oscillatoria subbrevis all exhibited large summer populations. Anabaena circinalis was a dominant when its counts were still low, and the remaining four species were dominants as their populations waxed and waned. Coelosphaerium naegelianum showed summer peaks, then a decrease before increasing again to autumn peaks. It too was a dominant through low and high cell counts. The small Lyngbya lagerheimii filament occurred as a winter species and was a dominant then.

Stephanodiscus hantzschii was the one bacillariophycean algae to be a dominant (Figure 11). That dominant population occurred as the species peaked in spring of 1974. The cryptophycean alga Rhodomonas minuta showed independent spring, autumn, and winter

peaks (Figure 9). The large spring and winter populations were dominants.

The vertical distribution of algal divisions was irregular to even. But, the seasonal interplay of cyanophycean species and chlorophycean species was evident (Figure 12a). During spring, populations from the Chlorophyta, Bacillariophyta, and Cryptophyta were important. Then the Cyanophyta increased rapidly in summer to 90% or more of the total cell counts. The autumn phytoplankton consisted of decreasing cyanophycean counts and increasing chlorophycean counts that continued to increase through the winter.

The overall interaction of species with the physico-chemical environment was indicated by three diversity indices (Figure 12b). No distinct vertical distribution pattern was apparent for the indices. Seasonally, the species richness, evenness, and diversity tended to be low in summer and winter, and high in spring and autumn.

3.2.3. Standing Crop

Phytoplankton standing crop was determined as total cells/ml and as chlorophyll *a*/m^3. The two measures paralleled each other well, $r = 0.650$, $p < 0.01$ (Figure 13), even though the samples originated from all depths.

Standing crop results, as measured by chlorophyll *a* content, are presented in a time-depth diagram (Figure 14a,b). Chlorophyll *a* tended to show slight, irregular changes with depth. A few exceptions did occur. On 29 September, 1974, an unusually high

Figure 12.
Seasonal distribution of algal divisions expressed on a percent composition basis (A) and seasonal distribution of species richness S, evenness E, and Shannon's diversity H (B) for the phytoplankton.

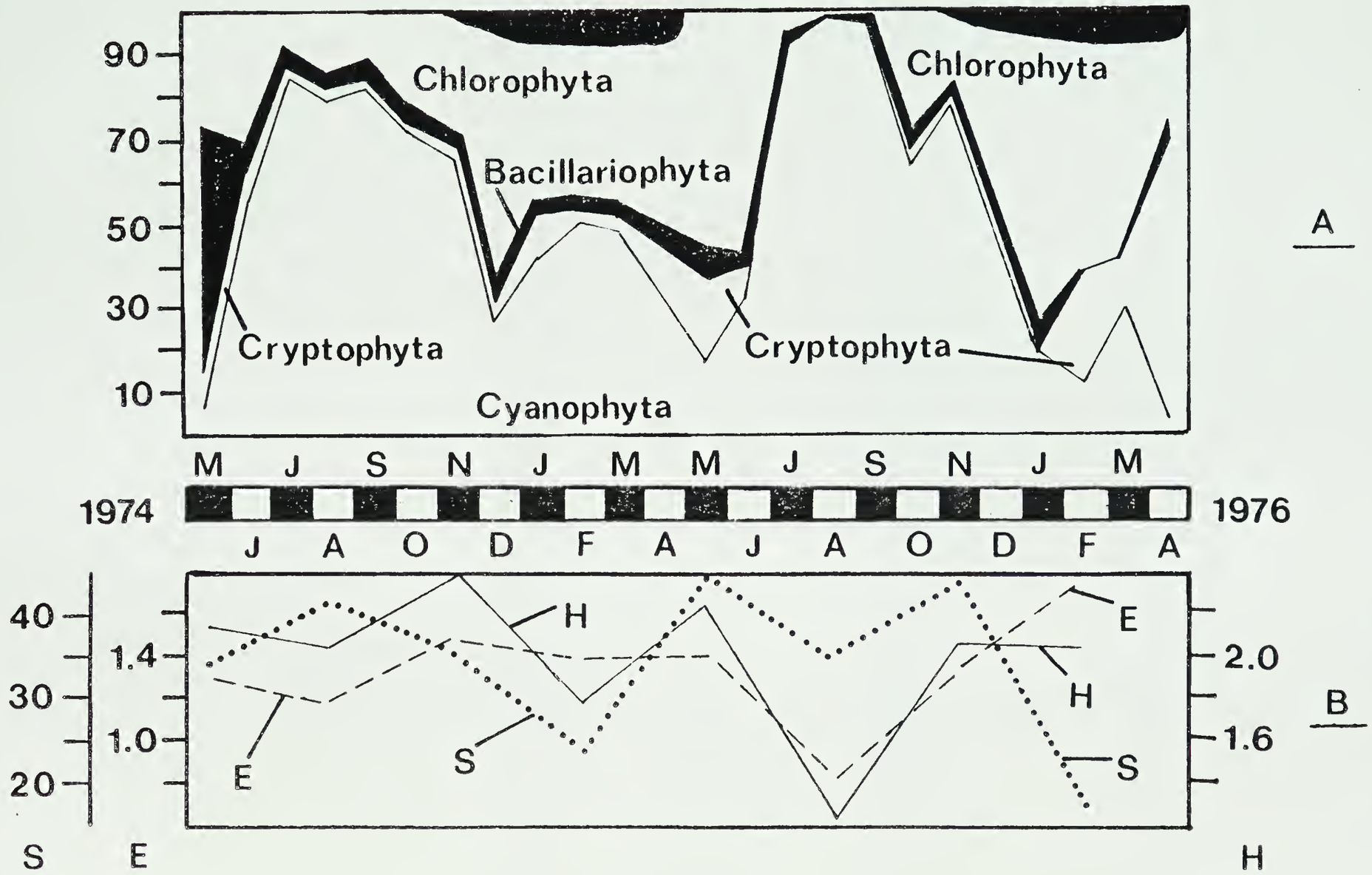

90
70
50
30
10
Chlorophyta
Bacillariophyta
Cryptophyta
Cyanophyta
Chlorophyta
Cryptophyta
A
M J S N J M M J S N J M
1974
1976
J A O D F A J A O D F A
40
30
20
1.4
1.0
S E
H
E
S
E
H
S
2.0
1.6
H
B

Figure 13.
Relationship between mg chlorophyll a/m^3 and total cells/ml x 10^4 for the phytoplankton.

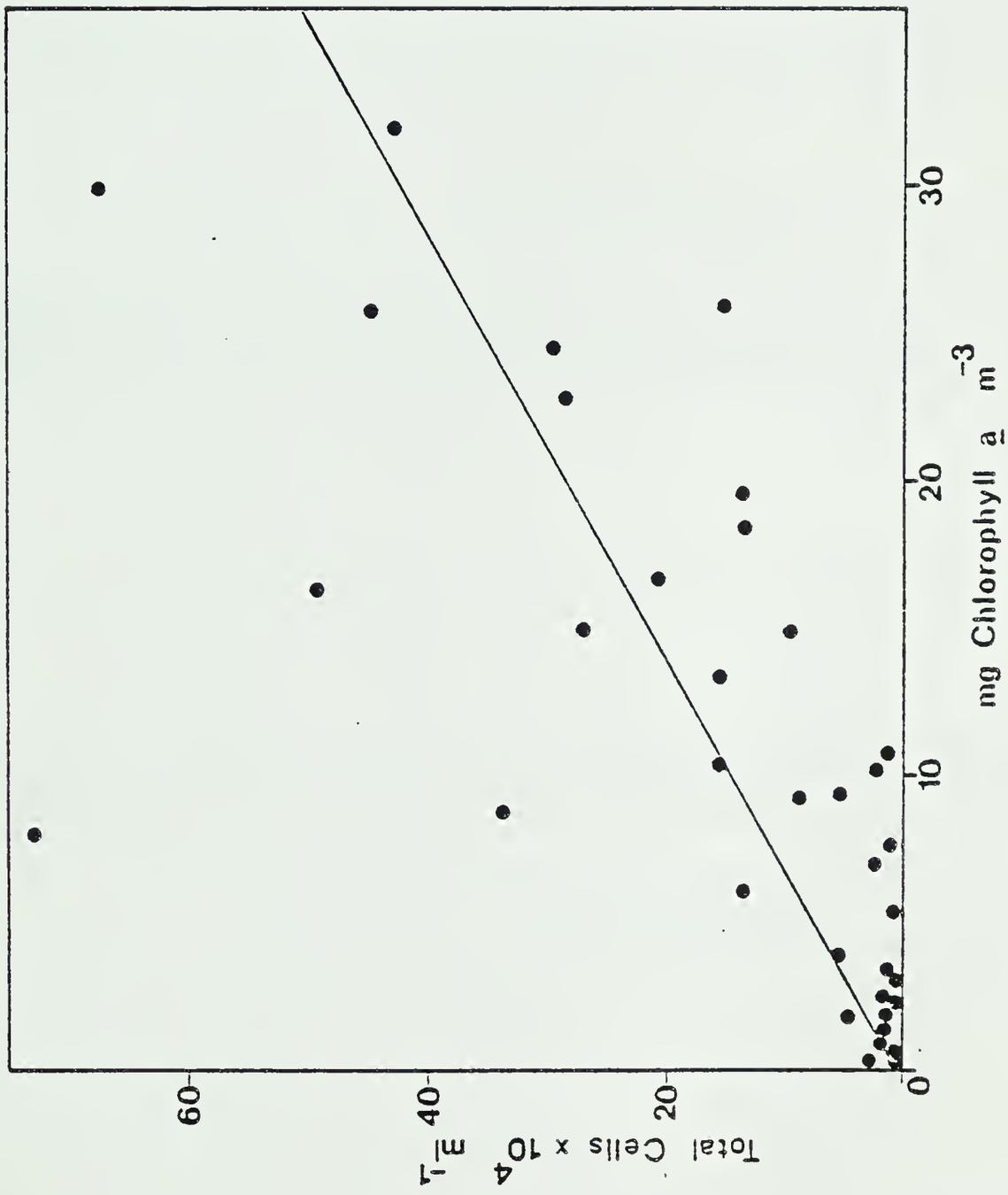
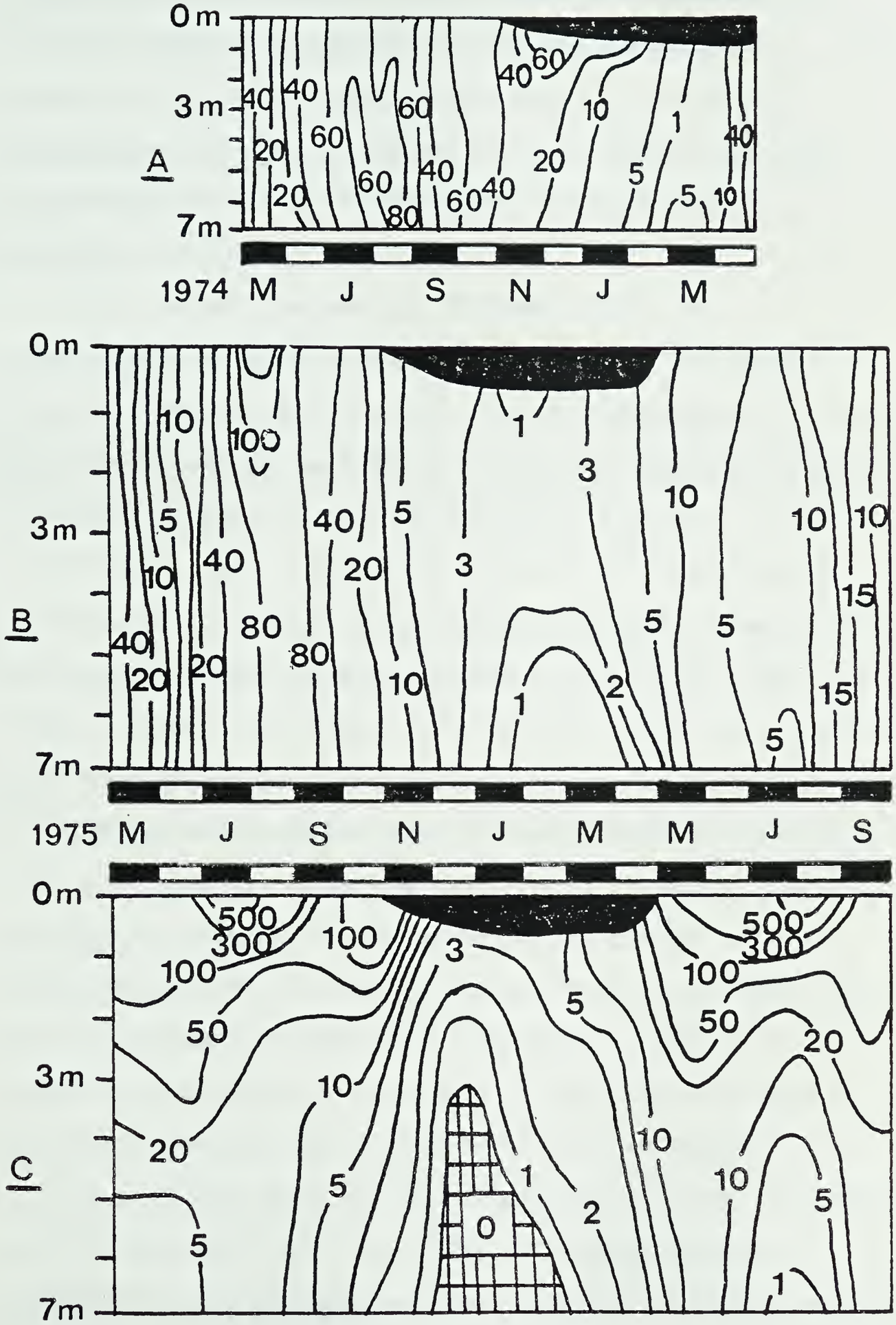

Total Cells x 10^4 ml^{-1}
0
20
40
60
0
10
20
30
mg Chlorophyll a m^{-3}

Figure 14.
Time-depth diagram of mg chlorophyll a/m^3 for phytoplankton 1974/1975 (A) and 1975/1976 (B). Time-depth diagrams of mg carbon/hr/m^3 for phytoplankton 1975/1976 (C).


0m
3m
7m
A
1974 M J S N J M
B
1975 M J S N J M M J S
C

value of 316 mg chlorophyll a/m^3 was found at 0 m where 28,122 cells/ml Anabaena flos-aquae formed the dominant population. A like situation followed on 5 August, 1974, when 213,301 cells/ml Botryococcus sudeticus and 108,136 cells/ml Anabaena flos-aquae co-dominated the 0 m collection which accounted for 134 mg chlorophyll a/m^3.

Under ice on 1 December and 9 December, 1974, an uncharacteristic steady decrease in chlorophyll a with depth was recorded. On these two occasions, dominant Chlamydomonas spp., with cell counts ranging from 5,837 to 424 cells/ml, possessed vertical distributions which followed the chlorophyll a profile. Under ice on 26 January, 1975, a relatively high value of 38 mg chlorophyll a/m^3 occurred with 5,094 cells/ml Rhodomonas minuta as the dominant. The same species was the dominant under ice on 6 April, 1976, with 42,697 cells/ml contributing to the relatively high 5 mg chlorophyll a/m^3 found at 1 m.

Lastly, on 6 September, 1976, a disproportionately high 136 mg chlorophyll a/m^3 was determined for 7 m where 359,380 cells/ml Microcystis aeruginosa formed the dominant population. Similar situations occurred with specific species counts, even though they were not reflected in chlorophyll a anomalies. Examples of these notable irregularities in the vertical distribution of community cell count standing crop are presented in 3.2.2. Species.

On a seasonal basis, the phytoplankton 0 m standing crop peaked at 46 mg chlorophyll a/m^3 in May 1974, with Stephanodiscus hantzschii and Chlamydomonas spp. as co-dominants. Through June as

standing crop decreased and then began increasing, there was an evident shift from bacillariophycean and chlorophycean to cyanophycean populations. In July, as standing crop steadily increased, Anabaena flos-aquae was succeeded by Anabaena circinalis as the major dominant. Microcystis aeruginosa replaced the Anabaena spp. as the dominant in the latter part of July, when a community standing crop maximum of 316 mg chlorophyll a/m^3 was recorded at 0 m. A subsequent steady decrease followed through August and September, then a slight increase developed into a peak of 80 mg chlorophyll a/m^3 early in October. Coelosphaerium naegelianum, Merismopedia tenuissima, and Oscillatoria subbrevis were co-dominants then. Ice formed during November, and as standing crop decreased, a shift from cyanophycean to small chlorophycean species occurred in December 1974. Chlorella vulgaris was the major dominant early in the winter when standing crop was low. This pattern continued January through March 1975, when a winter standing crop minima was recorded. The flagellated chlorophycean species Gonium sociale, Pandorina morum, and especially Chlamydomonas spp. were important dominants along with the flagellated cryptophyte Rhodomonas minuta as chlorophyll a slowly began to increase under ice in March and April 1975.

With spring ice break-up and turnover, a spring peak of 52 mg chlorophyll a/m^3 was recorded in May 1975, and Chlamydomonas spp. and Rhodomonas minuta were the important dominants. As standing crop slumped in June and then began to increase toward a summer maximum, a change from chlorophytes to cyanophytes was noted; all of

the July dominants were cyanophycean algae. A maximum of 117 mg chlorophyll a/m^3 was reached at 0 m in early August, and Aphanizomenon flos-aquae and Microcystis aeruginosa were dominants at that time. Following the summer maximum, a steady decrease carried into autumn with the cyanophycean dominants Coelosphaerium naegelianum, Gomphosphaeria lacustris var. compacta and Oscillatoria subbrevis complementing Microcystis aeruginosa populations.

As ice formed in November 1975, standing crop continued to decrease, reaching the winter minimum by late January 1976. During this time, the latter mentioned four cyanophycean species remained among the dominant populations at the lower depths with the largest population of Microcystis aeruginosa at 7 m. But also small chlorophycean species were co-dominant; these included Chlorella vulgaris, Kirchneriella contorta, and Selenastrum minutum. In addition, the chlorophycean flagellates Chlamydomonas spp., Gonium sociale, and Pandorina morum were dominants along with the cryptophycean flagellate Rhodomonas minuta. These flagellated species tended to remain near the top of the water column and became more and more important as the cyanophycean and chlorococcalean populations decreased late in the winter during February, March, and April 1976.

In May 1976 with no ice cover and increased circulation, a spring peak of 92 mg chlorophyll a/m^3 was present at 0 m with Chlamydomonas spp. as the dominant population. Cyanophycean species became dominants in June while standing crop decreased. Anabaena circinalis and Microcystis aeruginosa populations carried into the

summer a standing crop maximum of 166 mg chlorophyll a/m^3. Microcystis aeruginosa and Oscillatoria subbrevis then were co-dominants as standing crop decreased toward the end of September and the termination of the study.

Therefore, three years of data indicated a persistent pattern. First there occurred a spring standing crop peak dominated by flagellated chlorophytes and cryptophytes. There then followed a summer standing crop maximum dominated by vacuolated cyanophytes, and then an autumn peak of cyanophycean species occurred. Low winter values under ice were dominated by small chlorococcalean chlorophytes and cyanophytes early in the winter and flagellated chlorophytes and cryptophytes late in the winter. The consistency of this pattern was further shown with the repetition of some of the same species year to year.

3.2.4. Productivity

Phytoplankton primary productivity is presented graphically as mg carbon/hr/m^3 May 1975 through September 1976 (Figure 14c). Throughout the study period, primary productivity decreased with increasing depth. No relationship was found between the vertical distribution of productivity and that of chlorophyll a standing crop. The upper 3 m of the water mass accounted for 74.6% of the total lake volume, 74.6% of the phytoplankton chlorophyll a standing crop, and 96% of the total phytoplankton productivity. This is in contrast to the region 3 m to the lake bottom, which represented 25.4% of the lake volume and 25.4% of the phytoplankton standing

crop, but only 4% of the phytoplankton productivity. Below 3 m little productivity was evident; during the winter, under ice cover from December until February 1976, productivity was undetectable. On those occasions when standing crop maxima were at depths below 3 m, productivity continued to decrease with increasing depth, and no productivity maximum coincided with a standing crop maximum.

Primary productivity decreased with depth rapidly as light decreased. Light appeared to be an important limiting factor determining the vertical profile of productivity.

The seasonal periodicity for phytoplankton primary productivity included a spring peak, a summer maximum, and an autumn peak (Figure 14c). The peak in May 1975 followed spring ice break-up and turnover. Rhodomonas minuta, Chlamydomonas spp., and Gomphosphaeria lacustris var. compacta were dominant populations at this time. A rapid decrease in productivity occurred in June, then a rapid increase to a mid-July summer maximum of 575 mg carbon/hr/m^3. Cyanophycean populations were the dominant species, the most prominent being Microcystis aeruginosa along with Anabaena flos-aquae and Aphanizomenon flos-aquae. A slow decline in productivity occurred through the latter part of July and August, and in September a low was reached before a peak in October. Microcystis aeruginosa and Gomphosphaeria lacustris var. compacta were dominants during this autumn peak. Afterwards, primary productivity decreased to low winter values under ice and snow cover from early November 1975 through late April 1976. From December until late

February, productivity below 3 m was undetectable. Above 3 m activity was attributed to photosynthesis by populations of Chlamydomonas spp., Gonium sociale, Pandorina morum, Kirchneriella contorta, and Selenastrum minutum. Primary productivity increased during March and April 1976, even though the lake was still ice covered. Populations of Chlamydomonas spp. and Rhodomonas minuta were dominant during this period. In May 1976, after spring ice break-up and turnover, and with increasing light intensity, a rapid increase in productivity resulted in a May peak dominated by Chlamydomonas spp. A summer maximum dominated by Microcystis aeruginosa followed with 506 mg carbon/hr/m^3 recorded at the surface in August. Productivity declined sharply into September, at which time the study was terminated.

Seasonal peaks in spring then were dominated by small flagellates and cyanophytes. In summer and autumn, peaks were dominated by larger colonial cyanophytes. During the winter lull in productivity small flagellates were again important.

3.2.5. Cross Incubation Studies

The results for cross incubation studies are presented as functions of collection depth and incubation depth (Figure 15, Figure 16, Figure 17). Standing crop,

Figure 15.
Phytoplankton productivity (A) and photosynthetic index (B) as a function of collection and suspension depths for October 1975 through January 1976.

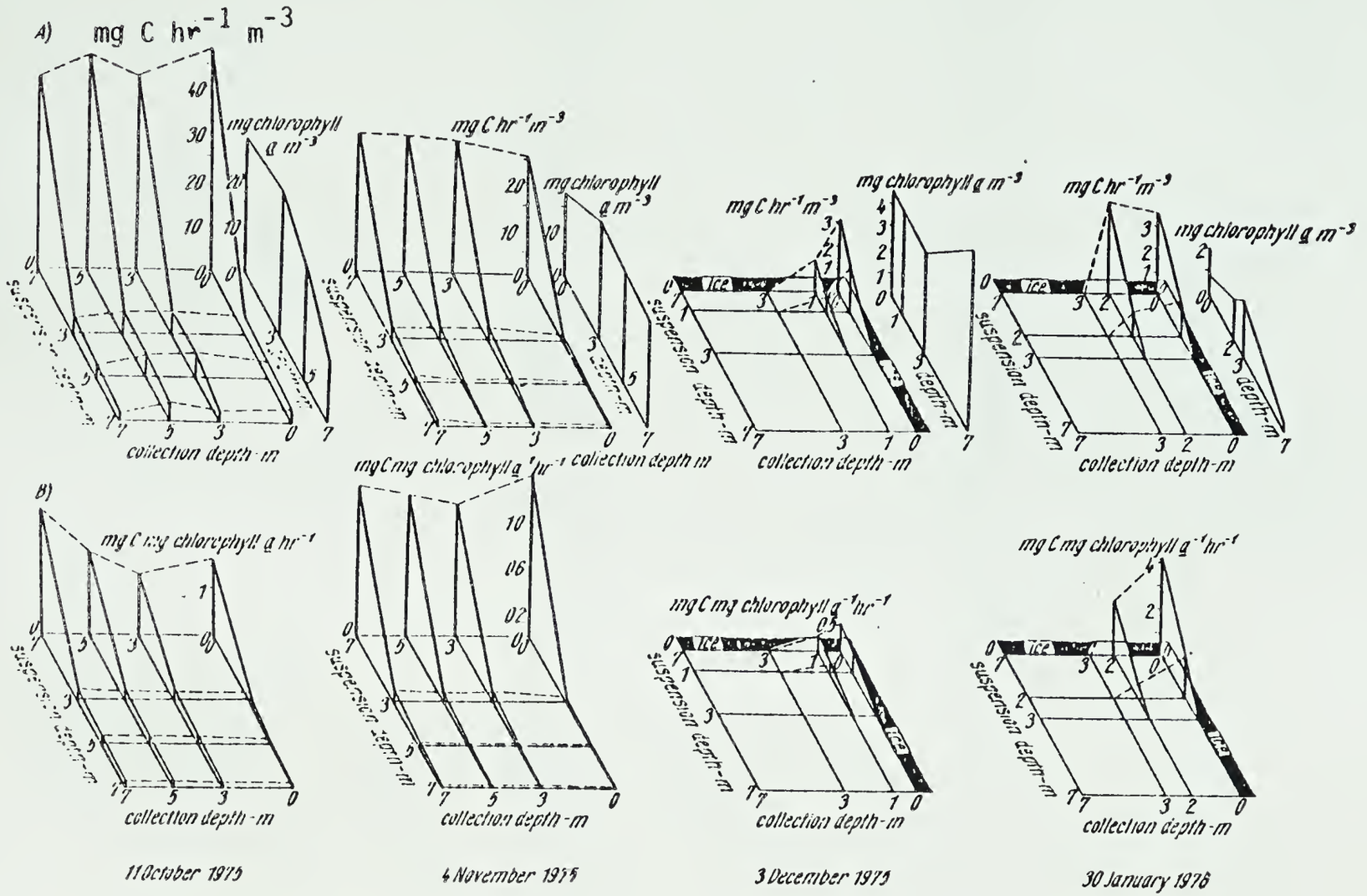

A) mg C hr⁻¹ m⁻³
mg chlorophyll a m⁻³
collection depth - m
mg C hr⁻¹ m⁻³
mg chlorophyll a m⁻³
collection depth m
mg C hr⁻¹ m⁻³
mg chlorophyll a m⁻³
collection depth - m
mg C hr⁻¹ m⁻³
mg chlorophyll a m⁻³
collection depth - m
B)
mg C mg chlorophyll a⁻¹ hr⁻¹
collection depth - m
mg C mg chlorophyll a⁻¹ hr⁻¹
collection depth m
mg C mg chlorophyll a⁻¹ hr⁻¹
collection depth - m
mg C mg chlorophyll a⁻¹ hr⁻¹
collection depth - m
11 October 1975
4 November 1975
3 December 1975
30 January 1976

Figure 16.
Phytoplankton productivity (A) and photosynthetic index (B) as a function of collection and suspension depths for March through June 1976.

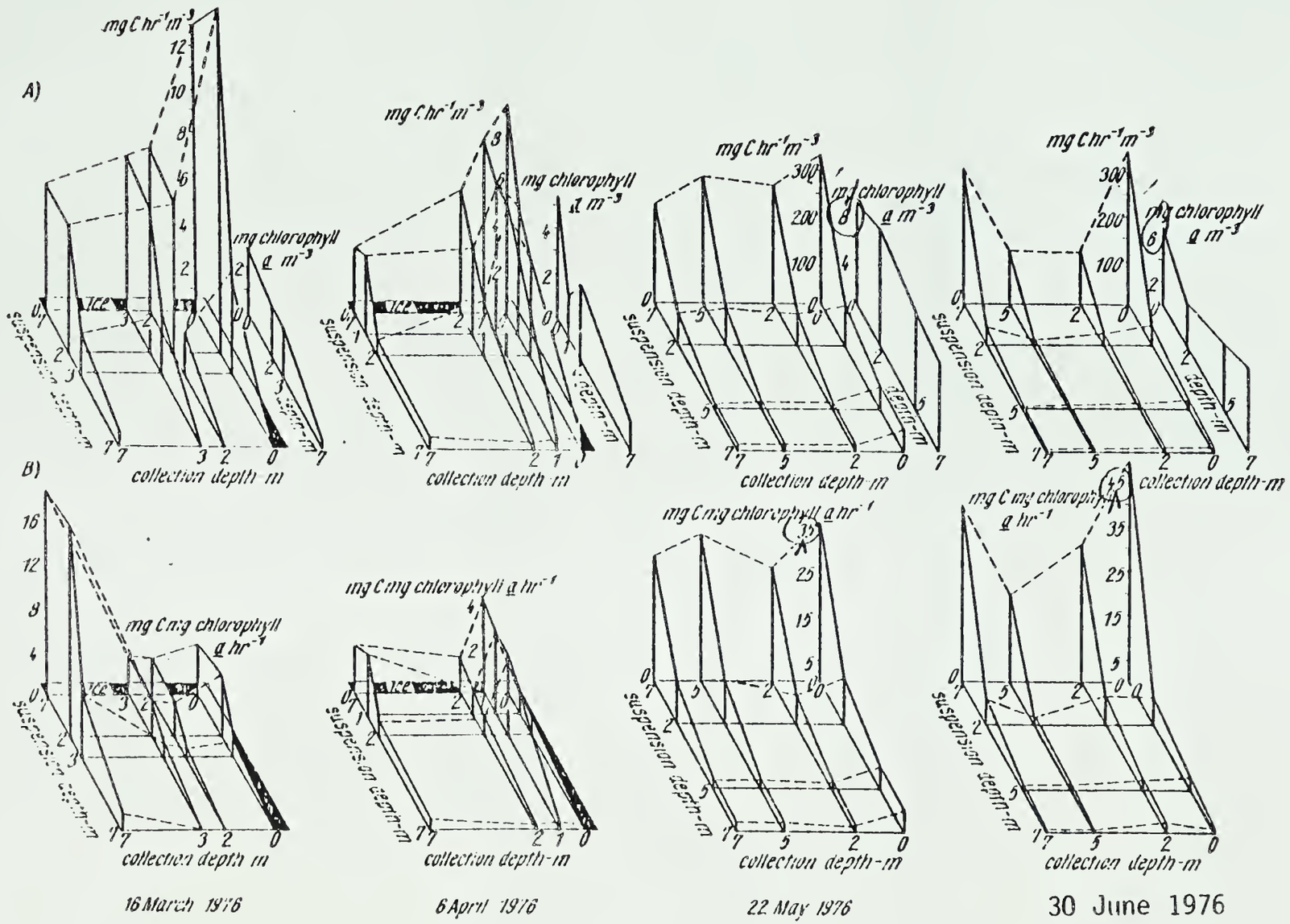
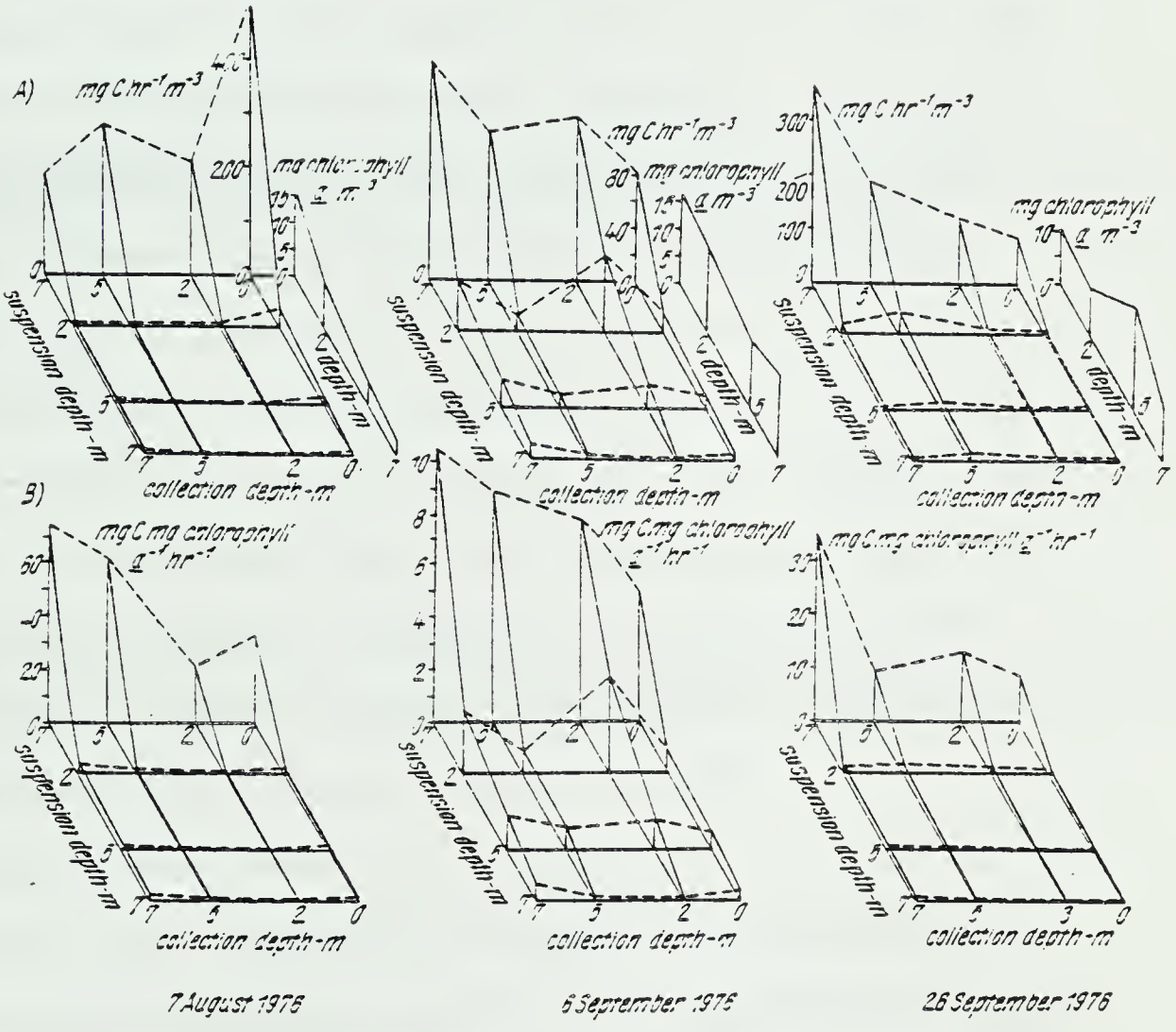

A)
B)
mg C hr⁻¹ m⁻³
mg chlorophyll a m⁻³
mg C mg chlorophyll a hr⁻¹
Ice
suspension depth-m
collection depth-m
16 March 1976
6 April 1976
22 May 1976
30 June 1976

Figure 17.
Phytoplankton productivity (A) and photosynthetic index (B) as a function of collection and suspension depths for August through September 1976.


A)
mg C hr⁻¹ m⁻³
mg chlorophyll a m⁻³
suspension depth-m
collection depth-m
B)
mg C mg chlorophyll a⁻¹ hr⁻¹
7 August 1976
6 September 1976
26 September 1976

productivity, and the photosynthetic index are expressed as mg chlorophyll a/m^3, mg carbon/hr/m^3, and mg carbon/hr/m^3÷ mg chlorophyll a/m^3, respectively.

Primary productivity and the photosynthetic index decreased with increasing depth on almost every sampling date (Figure 15, Figure 16, Figure 17). On 11 October, 1975, there was little difference among the productivity values of all samples incubated at 0 m. The standing crop decreased steadily with depth. Microcystis aeruginosa and Gomphosphaeria lacustris var. compacta were co-dominant populations at all collection depths with Oscillatoria subbrevis an additional co-dominant at 5 and 7 m. The relationship of the photosynthetic index to collection and suspension depths was of interest since the indices of the 5 and 7 m collections were greater than those of populations collected at 0 and 3 m when all were incubated at the surface. Then on 4 November, 1975, productivity and the photosynthetic index paralleled one another closely with respect to collection and suspension depths. Standing crop changes were slight with the smallest population found at 0 m. Again Microcyctis aeruinosa and Gomphoshaeria lacustris var. compacta were co-dominants at all collection depths.

By December, 1975, the lake was ice covered and the standing crop increased with depth. Chlamydomonas spp., Kirchneriella contorta, and Chlorella vulgaris were co-dominants at 0 and 1 m; whereas, Microcystis aeruginosa

and Gomphosphaeria lacustris var. compacta were co-dominants at 3 and 7 m. When samples were incubated just under the ice, only the populations from 0 and 1 m responded. These populations also responded when incubated at 1 m, but not at lower depths. The photosynthetic index showed the same pattern with the population collected at 0 m having the greatest index. A similar situation existed on 30 January, 1976. The standing crop maximum was at 3 m. Gomphosphaeria lacustris var. compacta was the dominant at 0 m, while it co-dominated with Microcystis aeruginosa at 2 and 3 m, and Microcystis aeruginosa alone dominated the 7 m collection. Only the populations from 0 and 2 m responded. The productivity of the 2 m collection suspended just under the ice was slightly greater than that of the 0 m collections incubated there. The photosynthetic index followed a like pattern, but the 0 m collection showed the highest index at the 0 m suspension. By 16 March, 1976, the flagellated algae Chlamydomonas spp., Gonium sociale, and Rhodomonas minuta dominated all depths as standing crop decreased with depth to a small biomass at 7 m. However, productivity was recorded at all suspension depths by all the populations. Below the 0 m suspension depth there was a sharp decrease in productivity for all populations. The photosynthetic index gave a different pattern as the populations collected from 7 m yielded the highest indices at all depths; whereas, there were few differences among the other collections at any given depth. Under ice on 6 April, 1976, a pattern similar to that of 16 March occurred even though the standing crop showed a more irregular distribution. Chlamydomonas

spp. dominated the 0 m collection, Rhodomonas minuta the 1 and 2 m collections, and Kirchneriella contorta the 7 m collection. The 7 m collection showed the smallest photosynthetic index, while the small biomass found at 1 m gave the highest index at all depths.

A study done on 22 May, 1976, after spring ice break-up, showed standing crop to be evenly distributed in the water column. Chlamydomonas spp. were dominant at 2 and 7 m, and co-dominant with Coelosphaerium naegelianum at 0 m and Kirchneriella contorta at 5 m. Primary productivity and the photosynthetic index responded similarly for all collection depths at respective suspension depths. All showed a sharp decrease when incubated below 0 m. This changed on 30 June, 1976, as populations collected at 0 and 7 m depths yielded higher productivity and photosynthetic indices than those collected at 2 and 5 m. The standing crops at 0 and 7 m were larger than those at 2 and 5 m. All depths were dominated by Anabaena circinalis and Microcystis aeruginosa populations. The standing crop decreased with increasing depth on 7 August, 1976 (Figure 17). Maximum productivity occurred when the populations from 0 m were suspended at 0 m. Other productivity values were variable; the populations collected from 5 m responded less than the 0 m collection, but more than the populations from 2 and 7 m. In contrast, the photosynthetic index of the 7 m collection was greatest followed by that of the 5, 0, and 2 m collections. On 6 September, 1976, the standing crop was evenly distributed, but with a slight decrease at 5 m. Microcystis aeruginosa was again the dominant species at 0 and 2 m and was a co-dominant with

Oscillatoria subbrevis at 5 and 7 m. The general pattern of productivity and its relationship with collection and suspension depths was again slightly irregular with the populations at 7 m accounting for the highest productivity value among all the collections suspended at 0 m. The trend of the photosynthetic index with respect to collection and incubation depths was more regular. The 0 m suspension depth was highest for 7 m populations, then 5, 2, and 0 m ones. A more variable relationship existed when populations were incubated at 2 m; here the collection from 2 m yielded the highest index. On 26 September, 1976, the final study showed standing crop irregular with increasing depth, and Oscillatoria subbrevis was the dominant algae at all collection depths. At 0 m, suspension depth productivity was highest for the 7 m populations, then the 5, 2, and 0 m ones. The photosynthetic index was similar with the 7 m collection highest at the 0 m suspension depth, but with the 2 m collection being slightly higher than the 5 and 0 m collections.

As shown, primary productivity and the photosynthetic index decreased with increased suspension depth, hence decreasing light intensity. Two exceptions did occur; both involved incubation of samples under ice. The first occurred on 16 March, 1976, when the sample collected from just beneath the ice gave a higher primary productivity value when incubated at 2 m than just under the ice. The second occurred on 6 April, 1976; on this occasion it involved the 7 m collection which showed its highest productivity at 1 m, not at 0 m. On both dates, the photosynthetic index paralleled

productivity. Although no evidence of surface light inhibition occurred in normal time-depth studies of productivity, these cross incubation studies did indicate light inhibition indirectly.

3.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

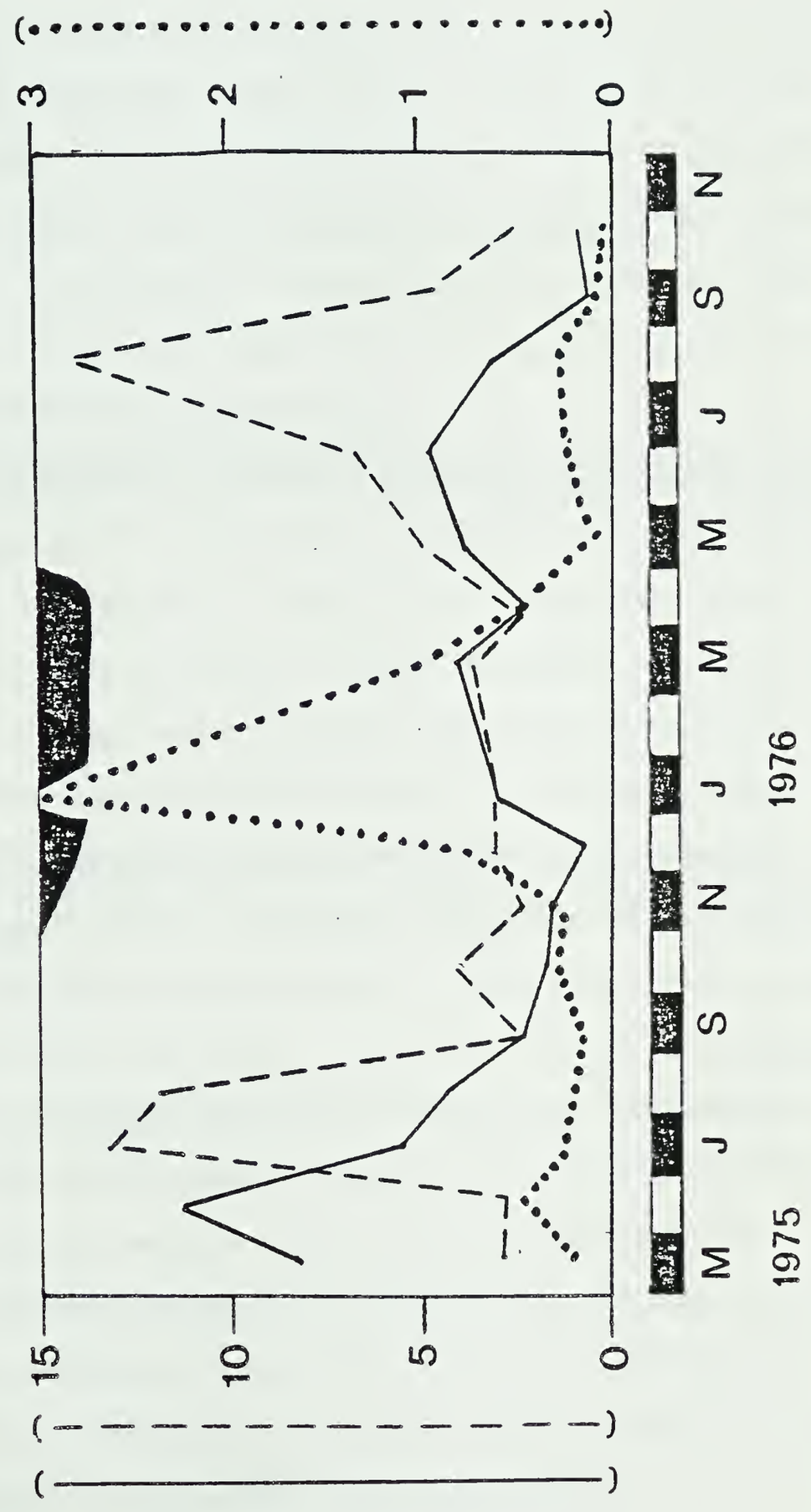
The photosynthetic index expressed as mg carbon/hr/m^3 ÷ mg chlorophyll *a*/m^3 is tabulated depth by depth and graphed seasonally for the 0 m depth (Table 4, Figure 18). The index was highest near the water surface, hence the region of highest light, and it decreased as depth increased. Seasonally the index was low in May 1975, then it sharply increased to a maximum of 45 by late June when *Anabaena flos-aquae* was the dominant population. A comparably sharp decrease followed into July and the index remained low through the summer and autumn. It decreased further until a minimum was recorded under the winter ice in December. From December 1975 through February 1976, in the lake region 3 m to the bottom, the index was zero due to the lack of detectable productivity. Then as the flagellated algae *Chlamydomonas* spp. and *Rhodomonas minuta* grew in importance, the index slowly increased just under the ice. After spring ice break-up, the increase quickened as spring populations of *Chlamydomonas* spp. were dominant. Then a rapid increase to a late June maximum of 50 occurred as *Anabaena circinalis* and *Microcystis aeruginosa* became co-dominants. During summer and autumn, a gradual decrease was noted.

The photosynthetic efficiency expressed as mg carbon/hr/m^3 ÷

Table 4. Mean photosynthetic index, photosynthetic efficiency, and productivity efficiency tabulated by depth for the phytoplankton during the May through October period of 1975.

	0 m	1-2 m	3-4 m	5-7 m
Photosynthetic Index	4.98	1.58	0.44	0.17
Photosynthetic Efficiency	6.62	126.60	166.65	250.00
Productivity Efficiency	0.12	2.37	3.19	6.75

Figure 18.
Seasonal distribution of
photosynthetic index (_____)
and photosynthetic efficiency (_ _ _),
and productivity efficiency (.....)
based on 0 m data
for the phytoplankton.


3
2
1
0
15
10
5
0
M J S N J M M J S N
1975
1976

cal/hr/cm^2 is tabulated as average values by depth and is graphed on a seasonal basis for 0 m data (Table 4, Figure 18). Efficiency increased as markedly with depth as light decreased; the values at 7 m were one hundredfold those at 0 m. Seasonally at 0 m, the photosynthetic efficiency showed summer trends to a peak of 14 in July of 1975 and 1976, with Microcystis aeruginosa the dominant in both years. In addition, on one winter date in February 1976, the efficiency spiked to a value of 16 when populations under the ice were dominated by Rhodomonas minuta.

The productivity efficiency expressed as mg carbon/hr/m^3÷(mg chlorophyll a/m^3 x cal/hr/cm^2) is tabulated as average values by depth and is graphed on a seasonal basis for the 0 m data (Table 4, Figure 18). The efficiency increased as markedly as light decreased with depth. Seasonal fluctuations showed two small pulses during the ice free seasons of 1975 and 1976, one in spring when Microcystis aeruginosa was co-dominant with Coelosphaerium naegelianum. However, the highest efficiency values occurred in January and February under winter ice when productivity, standing crop, and light were lowest. It was at this time that Chlamydomonas spp. and Rhodomonas minuta were co-dominants. Maintaining positions high in the water column near the ice, these small populations were able to utilize very low light intensities and carry on photosynthesis at productivity efficiencies relatively high in relation to those at other times of the year. That is they exhibited the ability to utilize available chlorophyll and available light more efficiently than other populations.

3.3. Discussion

3.3.1. Physico-chemical Parameters

Monthly means of incident irradiance showed summer values tenfold those of winter. As marked as the month to month differences were, steady decreases summer to winter and increases winter to summer occurred.

The penetration of impinging light into Hastings Lake was of particular interest. The euphotic zone, as defined by the 1% light transmission level, was restricted to the upper 0.5 to 3.5 m of the water column. This attenuation of incident irradiance can be considered an additive function of water color, ice and snow cover, suspended inorganic and organic detritus, and algal standing crop (Megard 1972, Lorenzen 1972, Steel 1974, Ganf 1974a,b, 1975). During ice free periods in Hastings, light attenuation was closely related to phytoplankton standing crop size, as the greatest reduction in light penetration occurred when high algal standing crop was present August to October 1974, August 1975, and July 1976. Yet the critical wave depth (Sverdrup, et al. 1942) established in Hastings by persistent winds during the ice free seasons was 3 m, and this was certainly enough to agitate considerable amounts of nonalgal material into the water column as well. During winter, the ice and snow cover reduced incoming irradiance to less than 10% before it reached the water just beneath the ice. The wind shifting of snow cover and changes in ice and snow texture can all influence the amount of light reaching the water, but generally 70 to 80 cm of snow will virtually darken all incident irradiance.

Calculations based on a linear regression between the light extinction coefficient and algal standing crop chlorophyll in Hastings indicated the algal material accounted for 51.3% of the light attenuation and the nonalgal material 48.7% (Hickman pers. com.). The rapid attenuation of light by both algal and nonalgal materials appears characteristic of Hastings Lake and other prairie-parkland lakes (Hickman 1979a,b,c).

As rapidly as incident solar radiation increased and decreased with the seasons, one might expect a like track for lake water temperature. Indeed, rapid spring heating and a rapid autumn cooling helped define environmental shock periods in Hastings and other prairie-parkland lakes (Hickman 1979a,b,c). The temperature curve was somewhat dampened in a two to four week lag behind the solar radiation curve, and the potential for vertical stratification was shown on occasional sampling dates during the ice free period. However, persistent wind turbulence permitted only slight temporary thermal stratification which did not establish any influential density gradients.

During the winter, under ice and snow cover, inverse stratification was noted with temperatures near 0 °C just under the ice and near 4 °C at lake bottom. There were slight fluctuations. Discrete pockets of warm, less dense surface water were noted under spring ice in Hastings (Potter 1977). Near the surface, variations may be due to changing incident irradiance and shifting snow cover. Temperature variation near the bottom may be the result of currents created by the influx of warmer water from the shallow, heated

littoral zone (Wetzel 1975), or from ground water flow into the lake (Schwartz and Gallup 1978).

The spatial and temporal distributions of oxygen in Hastings can be attributed to the effects of wind turbulence, algal photosynthesis, and bacterial respiration. During spring and fall, when algal photosynthesis was moderately high, the oxygen generated was enough, under the influence of wind turbulence, to keep percent saturation levels at, or near, 100% throughout the water column. Summer oxygen levels, expressed as means for the water column, decreased because the high saturation levels near the lake surface from algal photosynthesis were offset by saturation levels less than 50% near the lake bottom from bacterial decomposition of organic matter. This stratification occurred in spite of wind turbulence constantly mixing both layers, and so indicated the intensity of both the algal photosynthesis and the bacterial respiration. During winter as photosynthesis decreased, and ice and snow cover cut off exchange with the atmosphere, oxygen levels decreased. Here stratification was seen again, as small algal populations photosynthesizing under restrictive light conditions generated oxygen near the lake surface, and bacterial populations decomposing organic matter consumed oxygen near the lake bottom.

A similar situation existed for the spatial and temporal distribution of Hastings pH. The higher pH's near the top of the water column can be attributed to algal photosynthesis, and the lower pH's near the bottom of the lake can be attributed to bacterial decomposition. Within the pH range exhibited in Hastings,

photosynthesis takes CO_2 from HCO_3 yielding OH, and decomposition provides CO_2, which combines with OH yielding HCO_3. The pH stratification in summer, in spite of wind turbulence, again attests to the immediacy of the above reactions. Likewise, high summer pH's were probably due to high photosynthesis, and low winter pH's due to high decomposition.

An overview of spatial and temporal changes in the major chemical ions may be gained from data on specific conductance and bicarbonate (Lund 1957, Wetzel 1975). Both increased slightly with depth. Photosynthesis would deplete bicarbonate and other nutrients in the euphotic zone, and decomposition of organic matter would increase ion levels in the aphotic zone. Also, the low oxygen conditions accompanying decomposition would help reduce the oxidized microzone barrier on the sediment surface and ions would be released to the water column (Mortimer 1941, 1942, 1971). This is especially noteworthy in winter. Seasonal peaks of summer photosynthesis and winter decomposition would likewise help account for summer lows and winter highs in specific conductance and bicarbonate as composite representations of total ion fluctuations.

All four major cations indeed did show winter peaks, but sodium, magnesium, and potassium were relatively stable, while calcium showed marked changes. Although calcium has been shown to be an integral part of the inorganic carbon cycle and the co-precipitation of inorganic nutrients (Wetzel 1975), changes in Hastings concentrations were erratic and appeared not to be associated with any of the abiotic, or biotic, phenomenon monitored.

The anions sulfate, bicarbonate, and chloride also showed winter peaks; in contrast, carbonate showed a summer peak. Hastings seasonal sulfate results were surprising as increases were found with decreasing oxygen levels. Increased sulfate concentrations are most often associated with increased oxygen levels and the resulting oxidation of hydrogen sulfide (Wetzel 1975). It is possible that photo-autotrophic sulfur bacteria, anaerobes that photosynthesize under low light conditions, could oxidize hydrogen sulfide to sulfate; however, such populations of bacteria tend to be short-lived and not likely to account for a winter season of high sulfate concentrations. Such populations were not observed in Hastings during the study, but records have been noted in other lakes within the Cooking Lake Moraine (Potter 1977). A direct positive relationship between sulfate and oxygen was found for vertical profiles in Hastings as both tended to decrease with depth.

As noted earlier, the other major anion, bicarbonate, increased as depth increased and showed high winter values. This pattern and the part bicarbonate plays in the inorganic carbon cycle links the ion inversely to photosynthetic uptake of carbon. In contrast, carbonate showed a summer peak. This was probably due to the increased summer pH shifting the equilibrium of carbon species toward carbonate, though concentrations were still low (Hutchinson 1957). The remaining anion chloride increased in winter also.

The micronutrients iron, manganese, and copper showed averages close to worldwide levels, but zinc levels were somewhat higher than average (Wetzel 1975). All then were in sufficient concentrations

to support algal growth. All appeared to be inversely associated with oxygen concentrations. Such situations have been linked to chemical redox reactions for inorganic iron and manganese on sediments (Mortimer 1971); however, copper and zinc fluctuations have been assigned more directly to the decomposition of organic matter (Riley 1939).

Silica concentrations in Hastings were low to moderate (Wetzel 1975), but certainly enough to support diatom populations. The interrelationship between silica and diatoms is mutually paramount with respect to their distributions (Jorgensen 1957, Lund 1964, Tessenow 1966). Yet the vertical distribution of silica revealed only a limited association with diatoms during the springs of 1975 and 1976, and on a seasonal basis, little correlation could be found between silica and overall diatom populations. The physico-chemical effects of decreased oxygen, decreased pH, and relatively increased temperature near lake bottom on silica solubility were evident in winter as concentrations emanating from sediments increased greatly. A summary of silica and diatom populations from the phytoplankton, the epipelon, and the epiphyton is presented later (6.1.1. Physico-chemical Parameters).

Nitrate and ammonia are the two forms of nitrogen assimilated by most algae (Lewin 1962). Only nitrate was monitored as part of this study; nitrate is generally considered to follow ammonia inversely as oxygen levels increase and optimize the activity of nitrifying bacteria (Hutchinson 1957, Gode and Overbeck 1972). But in Hastings, during the ice free seasons, nitrate increased with

depth. This occurred even when oxygen decreased with depth, as oxygen concentrations may not have become so low as to become critical for nitrification (Wetzel 1975). But, the assimilation of nitrate by algal populations could account for reduced concentrations near the surface and for reduced values during the ice free season. During winter, under ice, as decomposition became more and more important, oxygen concentrations did approach critical levels deep in the water column restricting bacterial nitrification of ammonia to nitrate. Nearer the lake surface under ice, small populations of algae utilized some nitrate, but also created enough oxygen through photosynthesis to accomodate the oxidation of ammonia to nitrate. So, from the large decomposition source, ammonia was oxidized and accumulated as nitrate to become seasonal maxima in the upper oxygenated layers of the water column as winter nitrate concentrations decreased with depth.

However, the winter increase in nitrate and all the aforementioned ions, with the exception of carbonate, may be due, at least in part, to the selective exclusion of chemical species from lake ice during freezing (Bennington 1963, Schwartz and Gallup 1978). Hastings ice accounted for 29% of the total lake volume, but the ice possessed only about 3% of the electrolytes found in the surface water before freezing (Potter 1977). That is, 97% of the electrolytes in the surface water were displaced into the remaining 71% of the lake volume as ice was formed. However, vertical distribution studies generally did not indicate the ice in effect being a source as freezing occurred. Nitrate was a possible

exception as it appeared to emanate from the ice in time-depth diagrams, but the increase in surface nitrate concentrations did not occur early in the winter when ice was forming, as one might expect, but rather, later on when the ice was stable. Still the possibility existed for nutrient enrichment, as ions may be excluded preferentially (Goldman 1970, Groterud 1972, Daborn and Clifford 1974, Schwartz and Gallup 1978).

The distribution of orthophosphate in Hastings was a function of abiotic and biotic factors. Spring and autumn wind turbulence mixed concentrations evenly through the water column. During summer, an increase with depth occurred due to the combination of algal assimilation during photosynthesis in the euphotic zone (Kuhl 1962, Lean 1973, Rigler 1973) and sediment release under low oxygen conditions in the aphotic zone (Mortimer 1941, 1942, 1971). Summer oxygen stratification in Hastings was most pronounced in 1974 with levels at 7 m being less than 5% saturation; it was in this summer that orthophosphate appeared to be released from the sediments. The summer of 1975 showed some stratification with saturation levels near 50% at 7 m, and late in the summer of 1976, stratification occurred with levels near 30% at 7 m. But, in neither of those years was there any evidence of summer orthophosphate release.

During both the winter of 1974/1975 and 1975/1976, an increase also occurred with depth. Concentrations in the upper portions of the water column beneath the ice were depleted to some extent by flagellated algal populations actively assimilating orthophosphate in the euphotic zone. Although these populations were not large,

they were composed of small unicellular algae that maintained growth rates through the winter. In addition, contrary to the situation suggested for the other nutrients monitored, much of the orthophosphate found in surface waters before freezing appeared to be retained in the ice (Daborn and Clifford 1974, Potter 1977). Oxygen levels less than 5% occurred near the sediments in both winters, and orthophosphate was released establishing a profile that increased with depth. These major winter releases accounted for annual maxima.

3.3.2. Species

Seven of the nine cyanophycean dominants peaked and were community dominants during summer when high temperature and light conditions and low nitrate concentrations occurred. Indeed, for those seven species, positive correlations against temperature and light tended to be good, and negative correlations against nitrate, though somewhat lower, were also significant.

Merismopedia tenuissima, a spring/summer species, showed significant coefficients as follows: temperature, $r = 0.630$, $p < 0.10$; light, $r = 0.530$, $p < 0.10$; nitrate, $r = -0.250$, $p < 0.25$. Anabaena circinalis exhibited a high positive correlation with temperature, $r = 0.740$, $p < 0.05$; a lower coefficient was shown against light, $r = 0.560$, $p < 0.10$; and a low, but significant, negative correlation existed against nitrate, $r = -0.300$, $p < 0.25$. For Anabaena flos-aquae a good positive correlation was found with temperature, $r = 0.640$, $p < 0.10$; against light the coefficient was

$r = 0.540$, $p < 0.10$; and against nitrate, a negative $r = -0.230$, $p < 0.25$ existed. Similarly, for Aphanizomenon flos-aquae, a good positive correlation was calculated against temperature, $r = 0.600$, $p < 0.10$; a lower coefficient was found for light, $r = 0.370$, $p < 0.25$; and a low, significant negative correlation was shown against nitrate, $r = -0.340$, $p < 0.25$.

The remaining three blue-green dominants carried large populations into the autumn. These were all positively correlated with temperature and light, and showed significant negative correlations with a broad range of nutrients. For Microcystis aeruginosa, significant coefficients were calculated against temperature, $r = 0.540$, $p < 0.10$; against light, $r = 0.430$, $p < 0.10$; then, against nitrate, $r = -0.320$, $p < 0.25$; carbon, $r = -0.280$, $p < 0.25$; and silica, $r = -0.230$, $p < 0.25$. For Oscillatoria subbrevis, the coefficients were as follows: temperature, $r = 0.260$, $p < 0.25$; light, $r = 0.170$, $p < 0.25$; carbon, $r = -0.670$, $p < 0.10$; nitrate, $r = -0.430$, $p < 0.10$; silica, $r = -0.430$, $p < 0.10$; and orthophosphate, $r = -0.400$, $p < 0.25$. Similarly, for Coelosphaerium naegelianum, a summer/autumn species, the correlations for temperature and light were positive, but too low to be significant and significant negative correlations against nutrients were shown as follows: carbon, $r = -0.590$, $p < 0.10$; silica, $r = -0.470$, $p < 0.10$; nitrate, $r = -0.460$, $p < 0.10$.

Two cyanophycean algae were dominants during winter, Gomphosphaeria lacustris var. compacta and Lyngbya lagerheimii. Although the Gomphosphaeria species peaked in spring and autumn, its

winter dominance was reflected in negative correlations with temperature and light, as was the case for the Lyngbya species. Gomphosphaeria lacustris var. compacta showed a significant negative correlation with temperature, $r = -0.430$, $p < 0.25$, and a low but significant negative correlation with light, $r = -0.250$, $p < 0.25$. For Lyngbya lagerheimii temperature showed a significant negative correlation, $r = -0.490$, $p < 0.10$, while light exhibited a negative, but not significant, correlation, $r = -0.040$, $p > 0.25$. In addition, the Lyngbya species was negatively correlated with silica, $r = -0.280$, $p < 0.25$.

Six of the eight chlorophycean dominants had largest populations in spring and autumn when rapidly changing temperature and light conditions occurred. However, it was in winter that these six were community dominants, thus showing the ability to successfully compete against other species during the stress of low temperature and light. Indeed, low but significant negative correlation coefficients were calculated for these species against temperature and light.

In addition, four of the six showed a positive association with nitrate. Chlorella vulgaris was negatively correlated against temperature and light, $r = -0.420$, $p < 0.10$, and $r = -0.440$, $p < 0.10$, respectively, along with a positive correlation against nitrate, $r = 0.250$, $p < 0.25$. Similarly, Selenastrum minutum exhibited a negative coefficient with temperature, $r = -0.270$, $p < 0.25$, and a positive coefficient with nitrate and carbon, $r = 0.390$, $p < 0.25$, and $r = 0.350$, $p < 0.25$, respectively. Gonium sociale was

a third species to exhibit the negative relationship with temperature and light, and a positive relationship with nitrate as follows: temperature, $r = -0.510$, $p < 0.10$; then light, $r = -0.590$, $p < 0.10$; and nitrate, $r = 0.260$, $p < 0.25$. Finally, Pandorina morum also yielded negative correlation coefficients against temperature and light, but neither was significant; a positive correlation with nitrate was noted, $r = 0.410$, $p < 0.10$.

Two of those six showed a negative association with orthophosphate. Chlamydomonas spp. were negatively associated with temperature and orthophosphate, $r = -0.260$, $p < 0.25$, and $r = -0.300$, $p < 0.25$, respectively. Kirchneriella contorta was negatively associated with light, orthophosphate, and silica as follows: light, $r = -0.290$, $p < 0.25$; orthophosphate, $r = -0.320$, $p < 0.25$; and silica, $r = -0.410$, $p < 0.10$.

The remaining two chlorophycean dominants showed a positive relationship with temperature and light, and a negative relationship with nutrients. Crucigenia quadrata peaked in spring and was a community dominant then; the correlation coefficients for temperature and light were $r = 0.420$, $p < 0.10$, and $r = 0.640$, $p < 0.10$, while those for orthophosphate and silica were $r = -0.270$, $p < 0.25$, and $r = -0.430$, $p < 0.10$. Botryococcus sudeticus peaked in summer and was a community dominant then; here the coefficients for temperature and light were $r = 0.290$, $p < 0.25$, and $r = 0.480$, $p < 0.10$, and the coefficients for nitrate and carbon were $r = -0.360$, $p < 0.25$, and $r = -0.240$, $p < 0.25$.

Two other species were considered dominant in Hastings

phytoplankton. First, the cryptophyte Rhodomonas minuta showed peaks in spring, autumn, and winter, and it was a community dominant in spring and winter. For this species, a weak but significant negative correlation existed with temperature, $r = -0.360$, $p < 0.25$, and a low nonsignificant negative correlation existed with light, $r = -0.180$, $p < 0.25$. The second species was the bacillariophyte Stephanodiscus hantzschii, which showed a spring peak and was a dominant then. There was virtually no association between this Stephanodiscus species and temperature, but a weak positive correlation was shown with light, $r = 0.320$, $p < 0.25$. Of greater interest were the significant negative correlations with orthophosphate and silica, $r = -0.240$, $p < 0.25$, and $r = -0.410$, $p < 0.10$, respectively. In contrast, although total phytoplankton diatoms showed a similar $r = -0.270$, $p < 0.25$, against orthophosphate, the same dependent variable against silica yielded only $r = 0.140$, $p < 0.25$. The overall association between diatoms in the phytoplankton and silica concentrations was not good (3.3.1. Physico-chemical Parameters).

The seasonal interplay of dominants from the Cyanophyta and Chlorophyta in Hastings was evident. The cyanophycean dominants showed summer population peaks and were dominants at that time. As a result, they were most strongly correlated with summer high temperatures. The blue-greens have been shown to have higher temperature optima than the algae of other divisions, so as temperature increased, the blue-green algae gained a competitive advantage. Large cyanophycean populations also showed a positive

correlation with incident irradiance in Hastings; however, members of the Cyanophyta have been shown to be quite tolerant of both high and low light conditions (Paerl and Ustach 1982, Van Baalen, et al. 1971, Hutchinson 1967). More importantly, perhaps, than the positive correlations with temperature and light, were the negative correlations with nutrients, namely nitrate. As spring and summer standing crops increased, a greater and greater demand was made for nutrients in the euphotic zone. The proportional importance for blue-green nitrogen fixation increased as nitrates decreased. This special ability of certain cyanophytes to deal with decreasing nitrate levels again placed them at a competitive advantage during summer (Paerl and Ustach 1982).

The chlorophycean dominants generally showed spring and autumn activity and were dominants during winter as well. A tolerance for winter low temperature and light was shown in negative correlations with those factors. Populations maintained a modicum of growth under low temperature and light and were dominants, out-competing the blue-greens as winter nitrate levels were high. Indeed, all the chlorophycean dominants, with the exception of Crucigenia quadrata and Botryococcus sudeticus, showed positive correlation with nitrate. Spring and autumn species responded to moderated temperature and light conditions with population peaks and community dominance again out-competing blue-greens as nitrate levels were not at summer lows.

Thus, the temporal distributions of the dominant phytoplankton species were delineated by four shock periods (Round 1971, 1972).

The first shock period occurred with the coming of ice and stable winter conditions; then spring ice break-up began a period of turbulent changes; next set in a period of summer stability; and finally, increased autumn turbulence began. The intervening four seasons can be categorized in terms of algal species' response to temperature, light, and nitrate. From about the first week in November to about the first week in May, Hastings was ice covered. This accounted for four to five months of a comparatively stable winter environment, one which may be characterized by a relative lack of change around stressfully low temperature and light conditions, and high nitrate concentrations. With spring ice break-up, high wind turbulence created a constantly changing environment, but one which moderated winter temperature and light stress. This short one to two month spring season gave way to summer conditions by July, when for three to four months, relatively little change occurred around high temperature and light, and low summer nitrate levels. During October, autumn winds increased turbulence again, and another short period of quickly changing temperature, light, and nitrate conditions moderated summer nitrate stress.

The phytoplankton community's interaction with its environment can be reflected by species diversity indices (Deevey, Jr. 1969, Whittaker 1972, Hill 1973, Eloranta 1976). The indices have been associated with a variety of parameters, but sometimes interpretation has been difficult (Dickman 1968, Sager and Hasler 1969, Hurlburt 1971, Winner 1972, Brown 1973b). It is not the

intent of this study to compare diversity results with other studies, because differences in sample size, number of replicate samples, and utilization of index formulas further complicate interpretation. Rather, the changes in diversity are here related to environmental stability and stress within the phytoplankton, and later related in as like a manner as possible to conditions within the epipelon and epiphyton.

Species richness, evenness, and Shannon's diversity are assumed generally to increase as environmental stability increases (Buzas and Gibson 1969, Hill 1973, Peet 1974). In many studies, this has been reported as low diversity in winter and high diversity in summer (Margalef 1964, Goldman, et al. 1968, Anraku 1974, Eloranta 1976). In Hastings, winter and summer have been described as the most stable seasons. One may presume then that the stable winter period is subject to temperature and light stress, as stress tends to reduce diversity (Goulden 1969, Peet 1974). Furthermore, in Hastings one may assume that the stable summer period is also stressed, perhaps by nutrient depletion. Such summer conditions may be comparable to the lower indices attributed to eutrophic or polluted waters (Margalef 1964, Archibald 1972, Hallegraeff 1976), especially those associated with blue-green blooms (Boyd 1973). Thus, the resultant pattern in Hastings is low winter and summer diversity and high spring and autumn diversity.

3.3.3. Standing Crop

In this study a significant relationship between the two

standing crop measures, total cell counts and chlorophyll a, was found. For Hastings phytoplankton, there were relatively few dominant species and those did not differ too greatly in size. Even so, the phytoplankton was collected at different depths and thus represented different populations under generally different physiological conditions, especially light. Chlorophyll a content in algal cells can be affected by such factors; diurnal and even hourly changes in quality and quantity can occur (Yentsch and Ryther 1957, Fogg 1963, Colton, Jr. 1972). Therefore, a poor correspondence between cell counts and chlorophyll a is not unusual (Hickman 1973, Okino 1973, Berger 1975). In some cases, cell counts will be closely correlated with chlorophyll a (Hickman and Round 1970, Hickman 1971a, 1978); however, with the above mentioned possibilities, it is advisable to have the two measures of standing crop as complements.

The vertical distribution of standing crop as measured by mg chlorophyll a/m^3 was irregular to even on virtually every sampling date. During the summer, the normal turbulent pattern resulting from daily winds acting on the shallow basin could be broken by consecutive calm sunny days. On these rare occasions, a build-up of cyanophycean algae would temporarily appear on the lake surface. This was evident only through casual observations early on mornings of sampling dates. Invariably by mid-morning sampling time, slight breezes would disturb the surface and begin to mix the water column. This irregular to even distribution of phytoplankton standing crop is typical of shallow lakes subjected to persistent winds (Okino

1973, Haertel 1976, Hickman 1979a,b,c). During winter, small concentrations by cell counts of algae just beneath the ice in Hastings did occur, but the respective low chlorophyll *a* levels were not appreciably higher than values elsewhere in the water column. Full profiles of cell counts and chlorophyll *a* decreasing with depth are feasible in Hastings, dependent on depth of snow cover (Maeda and Ichimura 1973, Lecewicz, *et al*. 1973).

Seasonal fluctuations in standing crop exhibited an increase under ice in late winter/early spring as has been noted in other studies (Lecewicz, *et al*. 1973, Larsen and Malueg 1976). Just after spring ice break-up, spring peaks occurred, followed by a slump before the summer maxima. The ensuing decrease was punctuated with indications of an autumn peak before winter minima were shown. This pattern is comparable to that of other shallow, eutrophic, prairie-parkland lakes, and it has been suggested that light and temperature are the prevalent factors controlling its development (Haertel 1976, Hickman 1979a,b,c). In Hastings, the correlation between standing crop total cells and incident solar radiation indeed yielded the highest coefficient calculated for standing crop, $r = 0.850$, $p < 0.05$. Of similar importance was the correlation between standing crop chlorophyll *a* and incident solar radiation, $r = 0.630$, $p < 0.10$. Furthermore, both total cell counts and chlorophyll *a* yielded the same significant coefficient against water temperature, $r = 0.770$, $p < 0.05$.

As strong as the relationships between standing crop, light, and temperature were, there were also significant correlations

against the major nutrients monitored. Standing crop total cells against bicarbonate, representing overall nutrient status (Lund 1957, Moss 1969b, Hickman 1978), yielded $r = -0.550$, $p < 0.10$, and standing crop chlorophyll *a* against the same independent variable yielded $r = -0.720$, $p < 0.05$. These significant correlations were reflected in the calculations of each standing crop measure against each of the major nutrients. Total cell counts against orthophosphate, nitrate, silicate, and available inorganic carbon showed $r = -0.640$, $p < 0.05$; $r = -0.500$, $p < 0.10$; $r = -0.760$, $p < 0.05$; and $r = -0.550$, $p < 0.10$, respectively. Chlorophyll *a* against orthophosphate, nitrate, silicate, and available inorganic carbon showed $r = -0.610$, $p < 0.10$; $r = -0.620$, $p < 0.10$; $r = -0.630$, $p < 0.05$; and $r = -0.720$, $p < 0.05$, respectively. Although such significant negative correlations suggest nutrient limitations, this is not necessarily the case (Haertel 1976). Algae possess the capacity for "luxury storage" of phosphate (Ketchum 1939, Gerloff and Skoog 1954) and use only a portion of the nitrate normally available to them (Holden and Caines 1974). Since neither phosphate nor nitrate are in short supply in Hastings, neither can be considered limiting. Still, strong negative correlations with nutrients are of note and certainly lend themselves to empirical equations for predictive purposes (Dillon and Rigler 1974, Hickman 1978).

Another factor sometimes discussed in relation to the seasonal fluctuations of phytoplankton standing crop is grazing. Many zooplankters are selective grazers, that is, small spherical

unicells are most commonly fed upon, presumably for physical reasons dependent on the anatomy of the zooplankters' feeding mechanisms (Wetzel 1975). Since it is possible for more than half the phytoplankton to consist of such smaller algae (Manny 1972, Kalff 1972), the effect of grazing on standing crop can be marked (Javornicky 1974, Gliwicz 1975). Furthermore, feeding for some zooplankters may be species selective (Pejler 1957) so affecting species succession and thus community standing crop. A study of planktonic rotifers in Hastings Lake suggested the spring peak of small "edible cells" may have slumped because of grazing by three Keratella species (Baker 1977).

Lastly, the potential for parasitism as a factor affecting Hastings phytoplankton standing crop was noted on a casual basis. Chytrid fungal parasites were observed during phytoplankton counting, most notably on the centric diatom Stephanodiscus rotula. Cells stocked with numerous chloroplasts and oil storage bodies, as well as cells virtually empty, were infected, but no obvious pattern of infection was recorded. The quantitative importance of such occurrences is not well understood, but studies indicate a possible influence on algal populations (Canter and Lund 1948, 1969).

3.3.4. Productivity

Phytoplankton productivity in nonstratified prairie-parkland lakes subject to wind turbulence appears to be more closely linked to light and temperature than to standing crop, nutrients, or other less cited parameters (Haertel 1976, Hickman 1979a,b,c). This was

most evident in Hastings with regard to the vertical distribution of productivity. The higher productivity values at the surface decreased rapidly with depth, hence decreasing light. No evidence of surface inhibition occurred, even during periods of highest light intensity, as has been reported in other studies (Edmondson 1956, Verduin 1956, Doty and Oguri 1957, Talling 1957, 1965, Jonasson and Mathiesen 1959, Goldman, Mason, and Wood 1963, Anderson 1964, Ichimura and Aruga 1964, Ichimura, Nagasawa, and Tanaka 1968, Croome and Tyler 1975, Eloranta 1976, Hickman 1979b). It has been suggested that cyanophycean populations in eutrophic situations may not display surface light inhibition under summer high light field conditions (Aruga 1965, Wetzel 1975, Eloranta 1976, Paerl and Ustach 1982). Under ice and snow cover in winter, Hastings productivity again decreased rapidly with depth as low incident irradiance rapidly decreased with depth.

Winter populations concentrated just beneath ice cover have accounted for varying productivity. In less extreme climates, such winter populations can make a significant contribution to total annual productivity (Maeda and Ichimura 1973). Ice thickness and snow depth in more northerly climates prevent penetration of low incident irradiance and thus limit productivity. As ice and snow cover deepen, productivity gradually decreases, till it becomes low to nil late in the winter (Schindler 1972, Schindler and Comta 1972). This pattern for northern lakes was seen in Hastings as productivity just under the ice decreased markedly from November through March and became undetectable in the lower portion of the

water column. During severe winters, when deep snow seriously blocks light penetration (Pennak 1968, Lecewicz, et al. 1973), eutrophic productivity might be supplemented by heterotrophy (Rodhe 1955, Wright 1964, Rodhe, Hobbie, and Wright 1966); however, it has been suggested that phytoplankton, especially flagellated species, physiologically adjusted to extremely low light conditions might still exist autotrophically with high productivity efficiency levels (Goldman 1970, Pechlaner 1971). In Hastings, primary productivity under ice cover began to increase in March and April coinciding with increased solar radiation and daylength. This early spring increase under ice has been noted in other northerly lakes (Schindler 1972).

Then, with spring ice break-up, there was the resumption of wind induced turbulence and isothermal conditions along with the rapid increase of incident irradiance. This marked change in the phytoplanktonic habitat was a seasonal shock period (Round 1971). There quickly followed a spring productivity peak with a change in species composition. The demise of many algae during the shock period is not surprising, because as has been suggested, species that live under ice over a long period develop high productivity efficiency gradually under steadily diminishing light conditions. The results are a shade type phytoplankton at the end of the winter, and the relatively quick change in the light regime that occurs as ice cover breaks up proves detrimental to many shade adapted species (Pechlaner 1971). In Hastings, only Chlamydomonas spp. and Rhodomonas minuta successfully readapted to the higher light intensities during spring. Large spring Chlamydomonas spp. were

found lower in the water column, as well as near the surface. Although this might be somewhat akin to winter flagellates migrating downward in the water column during spring to avoid supraoptimal light levels (Pechlaner 1971), it is more likely that the large Chlamydomonas populations were carried deeper into the water column by increased water circulation (Happey and Moss 1967, Hickman 1970, 1974, 1976a).

Summer conditions were established as light and temperature stabilized, nutrients became somewhat reduced by spring activity, and the opportunity for stratification, short-lived as it might have been, occurred in Hastings. It is then that cyanophycean algae often dominate eutrophic prairie-parkland waters and annual productivity maxima occur. In Hastings, the summer dominants Anabaena flos-aquae, Aphanizomenon flos-aquae, and Microcystis aeruginosa were alternately mixed through the euphotic zone and the nutrient enriched aphotic zone by intermittent, but persistent, wind turbulence. This effective use of the habitat resulted in summer productivity maxima.

In October, light and temperature began to decrease rapidly. It was then that Microcystis aeruginosa, along with two new cyanophycean dominants, Oscillatoria subbrevis and Coelosphaerium naegelianum, accounted for an autumn peak in productivity before the ice formed in November and winter conditions returned.

As light and temperature mark the four seasons in this northern continental climate, one might expect these parameters to be closely associated with the above mentioned productivity pattern in

northerly lakes (Gliwicz 1975, Wetzel 1975). Indeed, correlations between seasonal fluctuations of Hastings productivity and incident solar radiation were good; 1975, $r = 0.600$, $p < 0.05$; and for 1976, $r = 0.790$, $p < 0.05$. Similarly significant relationships between primary productivity and light intensity have been reported for other lakes (Goldman 1960, Goldman, et al. 1968). But the relationship is evidently variable, as less significant results have also been reported (Verduin 1957, Efford 1967, Dickman 1969, Hickman 1973). In addition, a significant correlation was found between seasonal fluctuations in Hastings productivity and temperature changes; 1975, $r = 0.850$, $p < 0.05$; 1976, $r = 0.660$, $p < 0.10$. Similar, though somewhat variable, results have been shown in other studies (Hunding 1971, Bindloss, et al. 1972, Fabris and Hammer 1975, Platt and Jassby 1976). Perhaps these variable responses are linked to relative light conditions; that is, if light intensity is low, productivity will not be temperature dependent, but if light intensity is high, productivity will be dependent upon temperature (Aruga 1965).

Chlorophyll *a* is another parameter often investigated in relation to productivity. In Hastings the correlation between the two was inconsistent; 1975, $r = 0.810$, $p < 0.05$; 1976, $r = 0.350$, $p < 0.25$. This lack of consistency was reflected in reports from other lakes, as a good relationship was found by some (Findenegg 1965, Javornicky 1974, Gliwicz 1975, Eloranta 1976) and a poor relationship by others (Winberg 1960, Hickman 1973).

Fluctuations of major nutrients have also been associated with

productivity. The most frequently cited elements are carbon (Paerl and Ustach 1982), nitrogen (Frink 1967, Boyd 1972), and phosphorus (Kerekes 1974, Ostrofsky and Duthie 1975). Phosphorus has been pointed out as an especially important factor controlling total annual productivity (Schindler 1974). However, for Hastings phytoplankton on a seasonal basis, there was little correlation between the orthophosphate and productivity; 1975, $r = 0.050$, $p > 0.25$. An interesting significant negative correlation did exist between productivity and nitrate; 1975, $r = -0.560$, $p < 0.05$. This inverse relationship has been reported in another field study (Goldman, et al. 1968) and has been associated with summer blooms of cyanophycean algae (Horne and Fogg 1970, Reynolds 1976). Considering bicarbonate as a measure of general nutrient status (Lund 1957, Moss 1969a, Hickman 1978) one must note the overall input of nutrients within the framework of light and temperature as indicated by a high negative correlation between productivity and bicarbonate; $r = -0.700$, $p < 0.05$. In shallow, eutrophic lakes such as Hastings, where wind turbulence mixes the standing crop alternately through the euphotic zone and the nutrient enriched aphotic zone, there is a very effective use of the habitat, and productivity is high (Ganf 1974a,b).

Grazing may also affect phytoplankton productivity (Davis 1954). Preferential feeding by rotifers on Hastings phytoplankton has been noted in a previous study (Baker 1977). Although grazing may stimulate the overall rate of productivity of small algae by keeping them in their exponential growth phase (Verduin 1957), such

feeding has been associated with the demise of phytoplankton populations, as the zooplankton populations peak (Gliwicz 1975, Wetzel 1975). Indeed, in Hastings, the slump between the spring peak and the summer maximum in productivity may be associated with the late spring burst of Keratella spp. feeding upon small flagellated species such as Chlamydomonas spp. and Rhodomonas minuta (Baker 1977).

3.3.5. Cross Incubation Studies

Cross incubation studies expanded primary productivity results. On 11 October, 1975, productivity profiles were quite different from those of the photosynthetic index. That is, although productivity increased equally for all collection depths when incubated at 0 m, the photosynthetic index for 5 and 7 m collections increased markedly at the 0 m suspension depth. The smaller populations found at 5 and 7 m were dominated by Gomphosphaeria lacustris var. compacta and Microcystis aeruginosa and were not senescent, but rather, quite capable of photosynthesis if brought to the surface by water circulation. The photosynthetic index may indeed vary within a community dependent upon specific component populations (Hillbricht-Ilkowska, et al. 1972). Certain algae exhibit higher potential per chlorophyll a biomass under light saturated conditions. Microcystis aeruginosa has been shown to be particularly active (Okino 1973). In addition, any one population will be comprised of three overlapping degrees of metabolic activity: organisms increasing in numbers, hence undergoing strong

anabolic growth; organisms maintaining more or less constant numbers over a period of time, hence undergoing only slight anabolic growth; and those organisms which are dying, hence decreasing in numbers (Soeder 1965). The overall affect on primary productivity and the photosynthetic index has been noted in other studies (Hillbricht-Ilkowska, et al. 1972, Hickman 1973, 1976a). The smaller populations at 5 and 7 m depths on 11 October, 1975, were dominated by metabolically active algae, not senescent ones. In contrast, the situation on 4 November, 1975, appeared simpler as the primary productivity and photosynthetic index paralleled one another with respect to collection depths and suspension depths.

Then, by 3 December, 1975, the lake was ice covered; there was a reduction in wind induced turbulence, and the standing crop increased with depth. The smaller populations collected just beneath the ice and at 1 m and dominated by chlorophycean algae, showed a positive response when incubated at 0 and 1 m. The larger populations, collected at 5 and 7 m and dominated by cyanophycean algae, did not respond when incubated at 0 and 1 m, and were obviously senescent. A similar situation existed at the end of January 1976. Then, in March 1976, a change occurred as flagellated populations collected just under the ice yielded the maximum primary productivity and photosynthetic index at the 1 m incubation depth. Also, the populations at 5 and 7 m were not senescent, but rather, quite active when incubated just under the ice. Thus, throughout the water column populations had changed and were physiologically adjusted to low light and low temperature. A like pattern was shown

by the phytoplankton under ice on 6 April, 1976.

In May 1976 after the ice had thawed, the primary productivity and photosynthetic index showed similar relationships with respect to collection and suspension depths. However, by the end of June, variable results indicated 0 and 7 m collections were comprised of a greater portion of actively growing cells than the 2 and 5 m collections. August productivity showed irregular patterns, and the photosynthetic index showed the most active populations were in the 7 m collection. Results for September were similar. The above mentioned variable patterns may well be expected in a lake where no thermal stratification occurs and intermittent but persistent wind induced turbulence is common. If populations remain at low light intensities deeper in the water column for as little as one to three hours, or as much as two to three days, temporary physiological adjustments in chlorophyll quantity and quality may depress the photosynthetic index when those collections are incubated at the surface (Yentsch and Ryther 1957, Yentsch and Lee 1966, Colton, Jr. 1972). Then, as cross incubations are done immediately before, during, or after frequent periods of water circulation, populations would be continually changing and variable metabolic states would exist in the profiles of the photosynthetic index.

3.3.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

Overall, the vertical aspect of the photosynthetic index showed a decrease with suspension depth for all collection depths (Elster

1965, Hillbricht-Ilkowska, et al. 1972, Hickman 1973), the variability of specific species size, diurnal cycles of chlorophyll quantity and quality, and seasonal changes notwithstanding (Okino 1973, Malone 1971).

The periodicity of the photosynthetic index has been linked to light, temperature, nutrient, and species fluctuations accounting for peaks in one or more of all four seasons (Saijo and Sakamoto 1964, Aruga 1965, Jorgensen 1970, Malone 1971, Hillbricht-Ilkowska, et al. 1972, Kalff 1972, Maeda and Ichimura 1973, Okino 1973, Eloranta 1976, Hickman 1976a, Platt and Jassby 1976). The sole spring peak in 1975 and 1976 displayed by Hastings phytoplankton was correlated closely with light and temperature; $r = 0.690$, $p < 0.10$, and $r = 0.770$, $p < 0.05$, respectively. The cyanophytes Anabaena flos-aquae, and Anabaena circinalis and Microcystis aeruginosa were the respective dominants late in spring of 1975 and 1976, reflecting their specific ability to adapt to high light intensities and available CO_2 (Paerl and Ustach 1982).

Algae have shown an apparent efficiency at utilizing low light conditions in the field for photosynthesis. For phytoplankton, photosynthetic efficiencies then tend to increase with depth and not to coincide with peaks in biomass, primary productivity, or the photosynthetic index (Dubinsky and Berman 1976). In Hastings the calculated photosynthetic efficiency of the phytoplankton certainly did increase rapidly with depth, hence decreasing light; however, on a seasonal basis, peak efficiencies occurred with high summer light conditions and the overall fluctuations correlated most closely with

bicarbonate, $r = 0.650$, $p < 0.10$, not light, temperature, or other nutrients. The high summer efficiencies, though not coincident, were certainly concomitant with high biomass, productivity, and photosynthetic indices. Furthermore, the dominant algae during the summer peak was the colonial mucilaginous species Microcystis aeruginosa, instead of solitary species which are often associated with high efficiencies (Okino 1973). But, too, a notably high photosynthetic efficiency was exhibited in winter for a single sampling date under ice with low light conditions and the solitary species Rhodomonas minuta was dominant. The apparent photosynthetic efficiency of the phytoplankton under field conditions appears associated with the interplay of many factors.

For Hastings phytoplankton, the productivity efficiency, that is, productivity per standing crop unit, per irradiance unit, showed a depth profile similar to that found in other eutrophic waters with a rapid increase from 0 to 1 m, then a slower increase with depth (Eloranta 1976). The interplay of light and nutrients may be more important in determining the seasonal aspect than temperature, or species (Platt and Jassby 1976).

In Hastings, seasonal fluctuations of productivity efficiency were most closely correlated with light, although the relationship was not linear. A logarithmic curve yielded a significant negative correlation, $r = -0.710$, $p < 0.05$. At light intensities less than 5 cal/hr/cm^2 under winter ice and snow, the efficiencies were high. Above this light level the efficiency decreased rapidly until light intensities reached about 25 cal/hr/cm^2, and then the decrease was

more gradual. At the sustained higher light intensities of summer, gradual changes in light saturation values may limit productivity (Goldman 1960, Elster 1965, Vollenweider 1965, Waite and Duthie 1974). The overall nutrient status as expressed by bicarbonate also yielded a significant positive linear correlation, $r = 0.650$, $p < 0.10$.

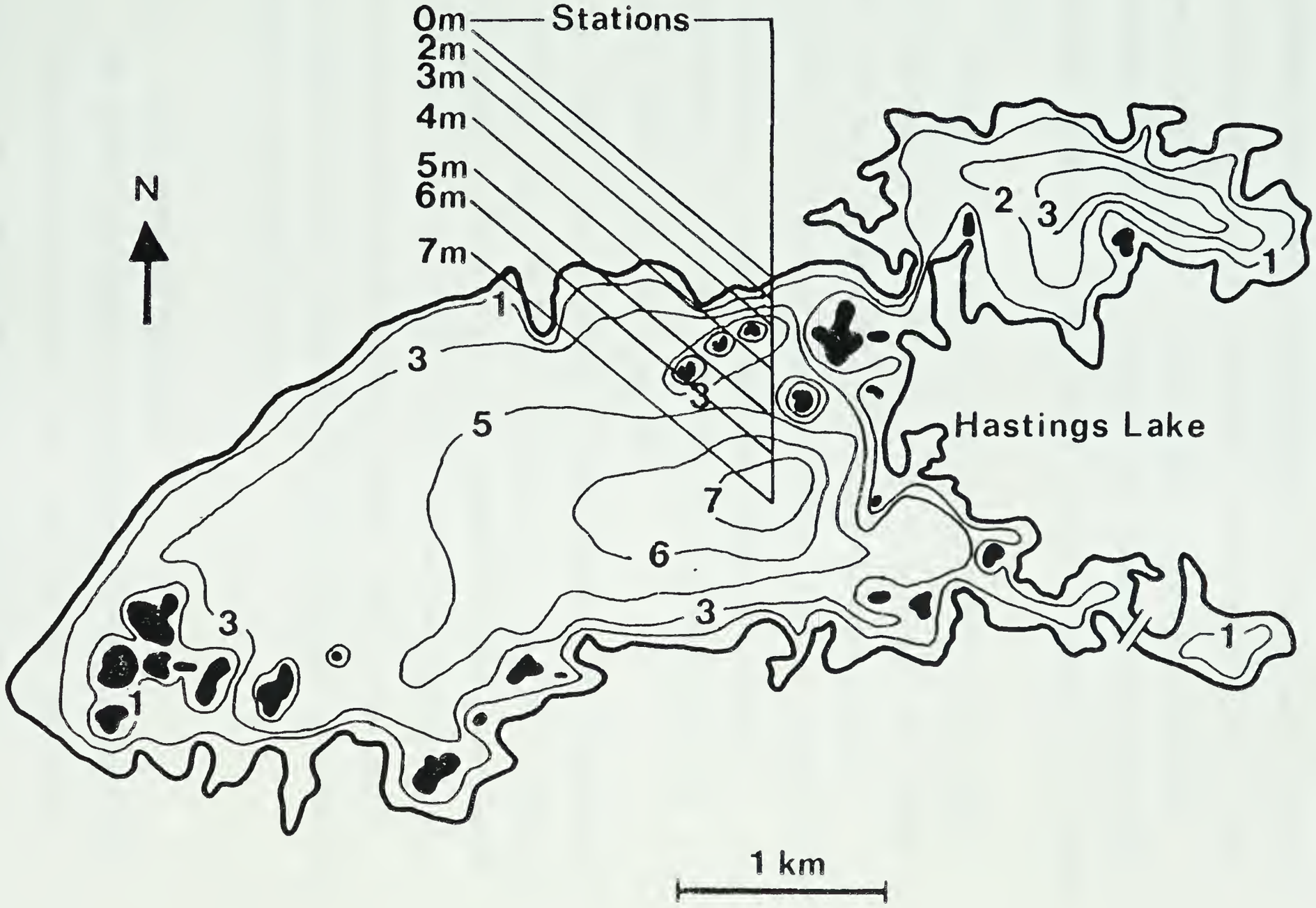
4. EPIPELON

The epipelon is that phytobenthic community consisting of algae populating sediment surfaces. For many years the epipelic algal community has been considered important in a variety of aquatic environments (Godward 1937, Lund 1942, Round 1955). Round (1964) and Moss (1977) have clarified characteristics of the community which delineate it from other algal communities. Yet relatively few studies have been done since a series of papers by Round (1957a,b,c, 1960, 1961a,b) Grontved 1962, Wetzel 1964, Moss 1967a, 1968, 1969b, Moss and Round 1967, Hargrave 1969, Hickman 1970, 1971a,b, Hickman and Round 1970, Gruendling 1971, Kowalczewski, et al. 1973, Moore 1974a,b,). Background for the general ecology of the epipelon in Canadian prairie-parkland lakes has been presented by Hickman (1974, 1976b, 1978). Therefore, in the study of Hastings Lake, it was decided to undertake a detailed investigation of physico-chemical parameters, species, standing crop, and primary productivity in the epipelon. A community overview would then allow comparisons with other algal communities found in the lake.

4.1. Methods

Sampling sites for the epipelon were along a transect running south from the north shore (Figure 19). Between 0 and 2 m depths, a sandy podzolic sediment was interspersed with decaying vegetation arising from the submersed hydrophytes Typha latifolia, Scirpus validus, Phragmites australis, Ceratophyllum demersum, Myriophyllum

Figure 19.
Bathymetric map of Hastings Lake showing sampling stations for the epipelon at 0 (0.25), 2, 3, 4, 5, 6, and 7 m depths.


0m
2m
3m
4m
5m
6m
7m
Stations
N
Hastings Lake
1 km

exalbescens, and Potamogeton vaginatus. A mixture of gyttja and decomposing Myriophyllum and Potamogeton occurred between 2 and 4 m, while beyond 4 m to 7 m, the sediment was flocculent gyttja, with some large stones at 6 m. Such changes in the substratum were reflected in the organic content of the sediment which varied from 3.5% at 0.25 m to 31.7% and 41.3% at 2 and 7 m, respectively (Figure 20a).

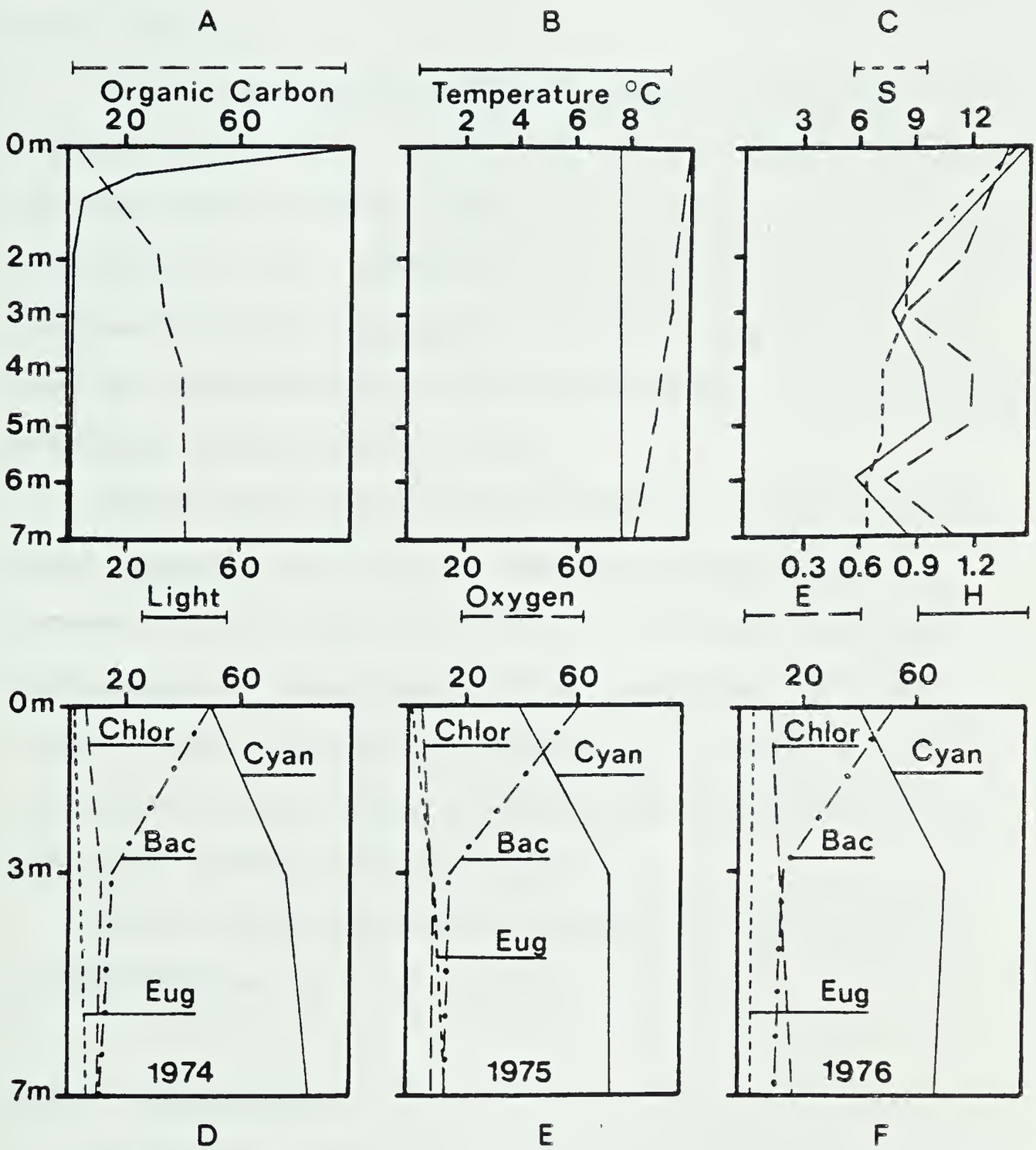
For the first two years of the study, epipelic algal samples were collected at depths of 0.25, 2, 3, 4, 5, 6, and 7 m. During the third year, one edge collection (0.25 m), one mid-depth collection (3 m), and one bottom collection (7 m), were made on each sampling date. The sampling schedule followed that of the phytoplankton as closely as possible, with the notable lack of winter epipelic productivity studies.

A sampling device designed for quantitative methods was used to collect four samples routinely from each site. Each set of four was mixed together in bulk to alleviate potential spatial heterogeneity within each site. The samples were collected and processed using the area based techniques of Eaton and Moss (1966). Sub-samples were taken for species identification and enumeration, chlorophyll a analysis, and productivity studies.

4.1.1. Physico-chemical Parameters

The spatial and temporal distributions of light as determined for the phytoplankton were utilized. Similarly, the temperature, oxygen, pH, and chemical analyses were gathered from 7 m

Figure 20.
Vertical distribution of percent organic carbon in sediments and percent light attenuation (A), of temperature and percent saturation oxygen (B), of species richness S, evenness E, and Shannon's diversity H (C), and of algal divisions for 1974 (D), 1975 (E), and 1976 (F) in the epipelon.


A
B
C
Organic Carbon
20 60
Temperature °C
2 4 6 8
S
3 6 9 12
0m
2m
3m
4m
5m
6m
7m
20 60
Light
20 60
Oxygen
0.3 0.6 0.9 1.2
E
H
20 60
Chlor
Cyan
Bac
Eug
1974
1975
1976
D
E
F

phytoplankton data. See 3.1.1. Physico-chemical Parameters for more detail.

4.1.2. Species

Species identification followed procedures presented for the phytoplankton in 3.1.2. Species. To aid in the identification of the large number of diatoms found in the epipelon, slides of cleaned frustules were made. Samples were cleared of organic matter by the addition of potassium dichromate and sulfuric acid; the frustules were then repeatedly washed with distilled water and finally mounted with Hyrax to make permanent slides.

Coefficients of variation were calculated for cell counts of whole samples and cell counts of dominant species selected to represent the four seasons as follows: spring total cells 29%, spring dominant Chlamydomonas spp. 36%; summer total cells 22%, summer dominant Coelosphaerium naegelianum 10%; autumn total cells 29%, autumn dominant Lyngbya lagerheimii 21%; winter total cells 45%, winter dominant Nitzschia palea 9%.

Species diversity indices were determined as those for the phytoplankton were in 3.1.2. Species.

4.1.3. Chlorophyll a

Standing crop chlorophyll a for the epipelon likewise was determined much as that for the phytoplankton (3.1.3. Chlorophyll a). Tissues and the entrapped algae were placed in an acetone extraction for spectrophotometric analysis and correction for

degradation products (Eaton and Moss 1966, Moss 1967a,b). The coefficient of variation calculated for the total method on samples from each of the four seasons was as follows: spring 19%, summer 25%, autumn 8%, and winter 41%.

4.1.4. Productivity

Productivity studies were restricted to the May through October ice free periods of 1975 and 1976. The carbon-14 method was adapted for the epipelon (Hickman 1970). Duplicate incubations were performed in situ from 1030 to 1430 hours utilizing a float system in conjunction with the phytoplankton incubations. The epipelic samples were processed just as were those of the phytoplankton, and expressed as mg carbon/hr/m^2. The coefficients of variation calculated for the total method of samples selected from three seasons were as follows: spring 10%, summer 8%, and autumn 11%.

4.1.5. Cross Incubation Studies

For cross incubation studies, samples were collected from the top of the euphotic zone (0.25 m), from the transition between the euphotic and aphotic zones (3 m), and from the bottom of the aphotic zone (7 m). Incubations of a collection at its respective depth as well as at every other collection depth, were performed to determine if populations living at deeper sites possessed the same, greater, or lesser photosynthetic capacity and efficiency as those from shallower water. Thus, the format from the phytoplankton cross incubation studies was followed (3.1.5. Cross Incubation Studies).

4.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

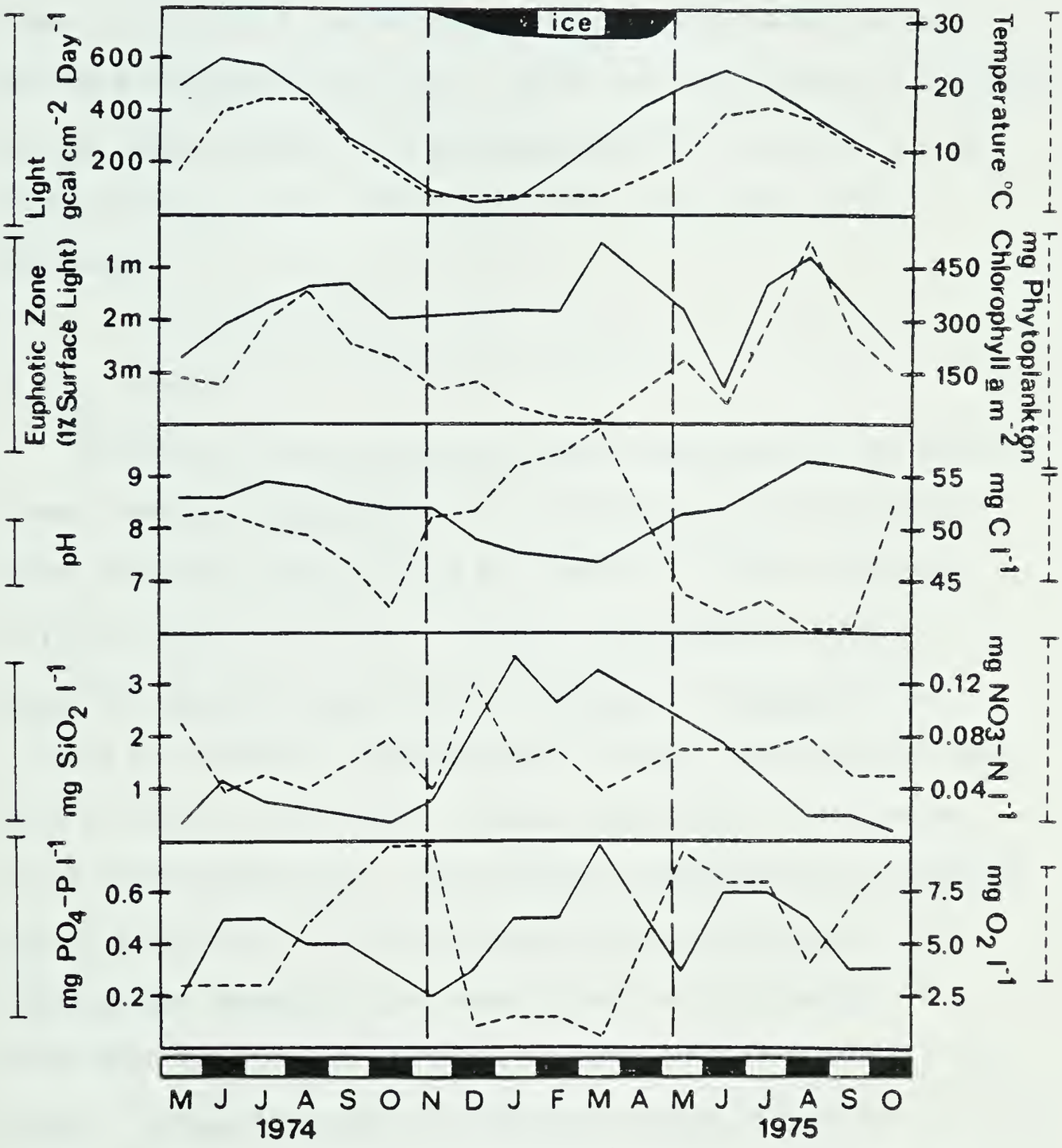
These functions were calculated for the epipelon as those for the phytoplankton were in 3.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency. Comparisons were intended among algal communities in Hastings Lake and only general comparisons were made with other studies.

4.2. Results

4.2.1. Physico-chemical Parameters

As noted earlier in 3.2.1. Physico-chemical Parameters, the attenuation of light in Hastings was rapid. The depth of the photic zone as defined by the 1% photosynthetically active radiation level was near 3 m in spring and autumn, and near 1 m in summer and winter (Figure 20). Water temperatures attained 20 °C in July each year and 4 °C during the winter (Figure 21); spring heating and autumn cooling was rapid. Dissolved oxygen values did not begin increasing until July 1974 and reached a peak in October before rapidly decreasing with the onset of ice and snow cover (Figure 21). Contrastingly, in 1975 they began increasing before complete ice thaw. The pH values fluctuated little, being lowest during the winter months and increasing each spring to reach a peak in late summer of 9.2 (Figure 21). Of the major nutrients, bicarbonate (carbon) increased under winter ice cover and rapidly decreased each spring as the ice thawed before falling more gradually through to autumn (Figure 21). Among the other three nutrients monitored

Figure 21.
Seasonal distribution of incident irradiance in gcal/cm^2/day, lake water temperature in °C, depth of euphotic zone as 1% incident irradiance, mg phytoplankton chlorophyll a/m^3, pH, bicarbonate as mg carbon/l, mg silica/l, mg nitrate/l, mg orthophosphate/l, and mg oxygen/l for the epipelon.


ice
Light gcal cm^{-2} Day^{-1}
600
400
200
Temperature °C
30
20
10
Euphotic Zone (1% Surface Light)
1m
2m
3m
mg Phytoplankton Chlorophyll a m^{-2}
450
300
150
pH
9
8
7
mg C l^{-1}
55
50
45
mg SiO$_2$ l^{-1}
3
2
1
mg NO3-N l^{-1}
0.12
0.08
0.04
mg PO$_4$-P l^{-1}
0.6
0.4
0.2
mg O$_2$ l^{-1}
7.5
5.0
2.5
M J J A S O N D J F M A M J J A S O
1974
1975

(Figure 21), nitrate was first to reach a maximum under ice cover. It was followed by orthophosphate and dissolved silica. The latter two reached maxima when oxygen levels were lowest. Nitrate-nitrogen levels fell late in the winter, and then reached maxima in the spring and autumn of each year. Dissolved silica generally declined to low autumn values, while orthophosphate was low in the spring before increasing to a summer peak after which values again decreased.

4.2.2. Species

Nineteen of one hundred eleven taxa encountered in the epipelon formed dominant populations, i.e., $\geq$ 20% of the total population based upon cell numbers (Table 5), and nine of these displayed distinct depth preferences. Navicula cryptocephala, Navicula gracilis, Navicula hungarica var. capitata and Achnanthes spp. (Figure 22, Figure 23) developed their largest populations at the 0.25 m site with only small irregular populations of each being found under deeper water. Both Navicula cryptocephala and Navicula gracilis exhibited June peaks; whereas, Navicula hungarica var. capitata and Achnanthes spp. were present in large numbers throughout the ice free periods with peaks in spring, summer, and autumn. Nitzschia gracilis and Nitzschia palea (Figure 23) occurred in greatest numbers at the 2 through 7 m sites, with largest numbers being found during the winter under ice and snow cover. Both these species co-dominated with the cyanophycean alga Oscillatoria subbrevis during the winter (Figure 24). Numerically, this

Table 5. Dominant species found in the epipelon.

CYANOPHYTA:

Anabaena flos-aquae (Lyng.) deBreb
Coelosphaerium naegelianum Unger
Lyngbya lagerheimii (Moebius) Gomont
Merismopedia tenuissima Lemm.
Microcystis aeruginosa (Kutz.) Elenkin
Oscillatoria subbrevis Schmidle

CHLOROPHYTA:

Chlamydomonas spp. Ehr.
Chlorella vulgaris Beyer
Crucigenia quadrata Morren
Dictyosphaerium pulchellum Wood
Pediastrum boryanum (Turp.) Meneghini

BACILLARIOPHYTA:

Achnanthes spp. Bory
Navicula cryptocephala Kutz.
Navicula gracilis Ehr.
Navicula hungarica var. *capitata* (Ehr.) Cl.
Nitzschia gracilis Hantzsch.
Nitzschia palea (Kutz.) W. Sm.

EUGLENOPHYTA:

Trachelomonas granulosa Playfair

Figure 22.
Seasonal distribution depth by depth of
Navicula cryptocephala, *Navicula gracilis*,
and
Navicula hungarica
var.
capitata
for the epipelon.

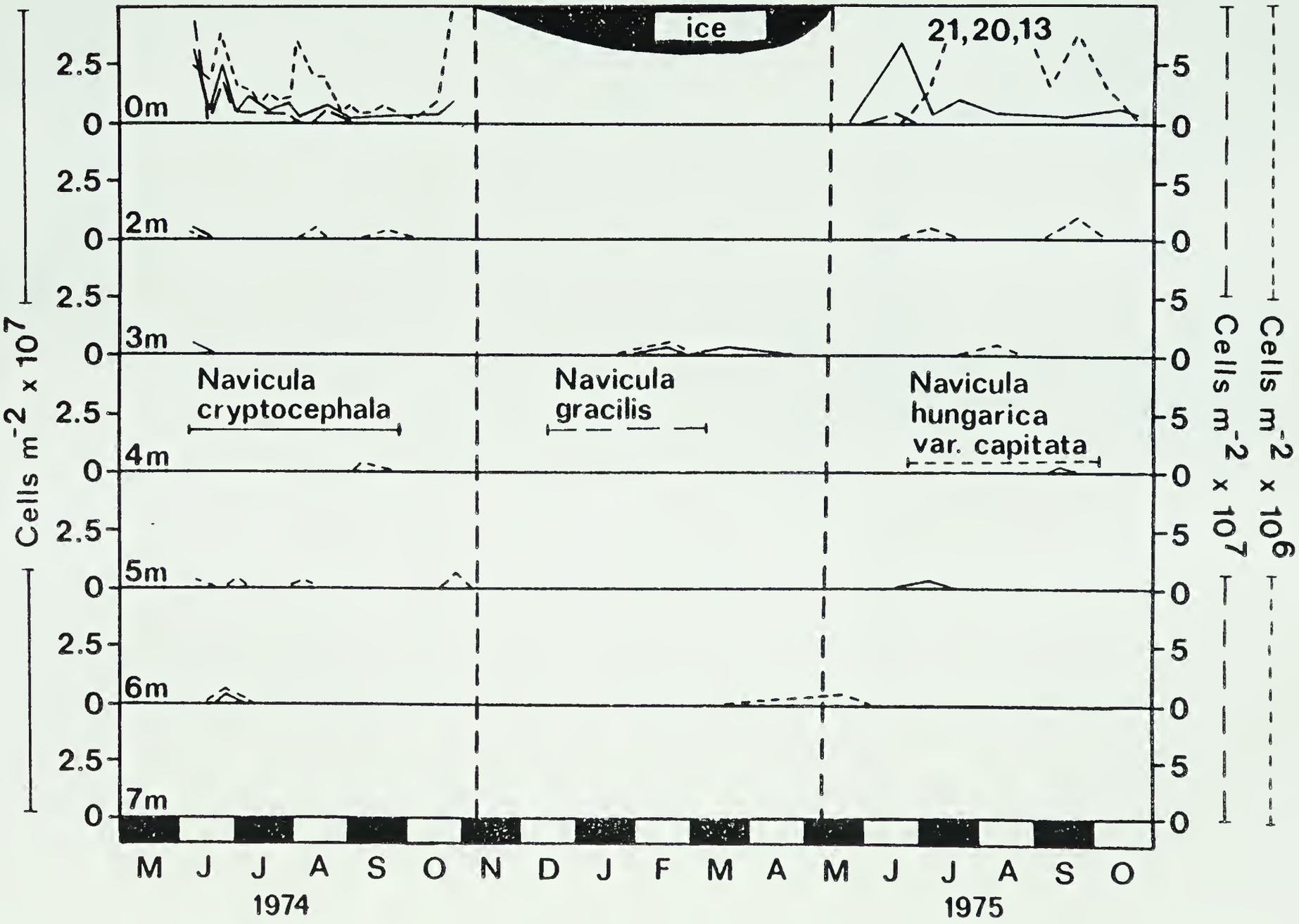

ice
21,20,13
0m
2m
3m
4m
5m
6m
7m
Navicula cryptocephala
Navicula gracilis
Navicula hungarica var. capitata
Cells m-2 x 10^7
Cells m-2 x 10^7
Cells m-2 x 10^6
M J J A S O N D J F M A M J J A S O
1974
1975

Figure 23.
Seasonal distribution depth by depth of
Achnanthes sp., Nitzschia gracilis,
and
Nitzschia palea
for the epipelon.

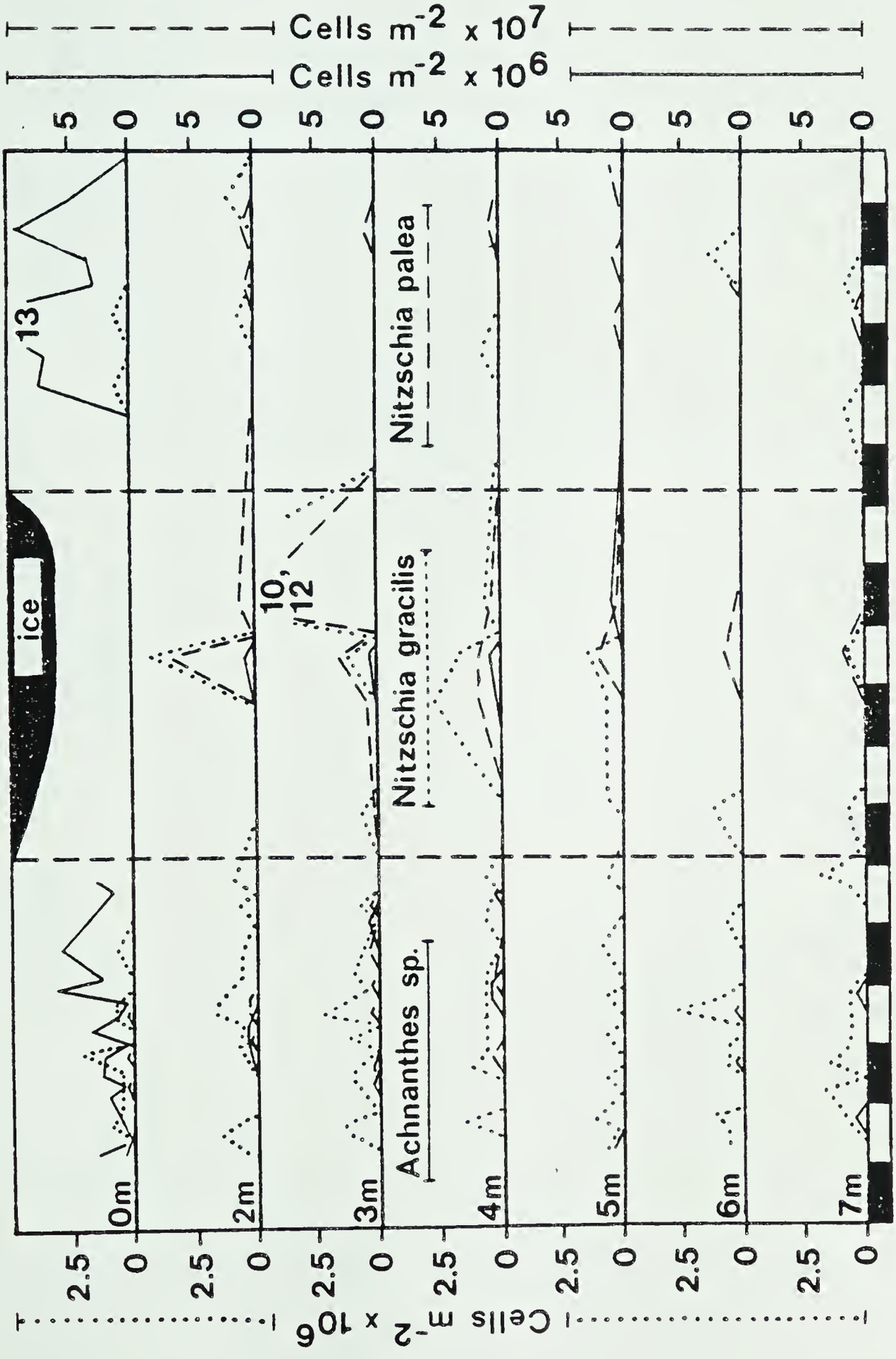
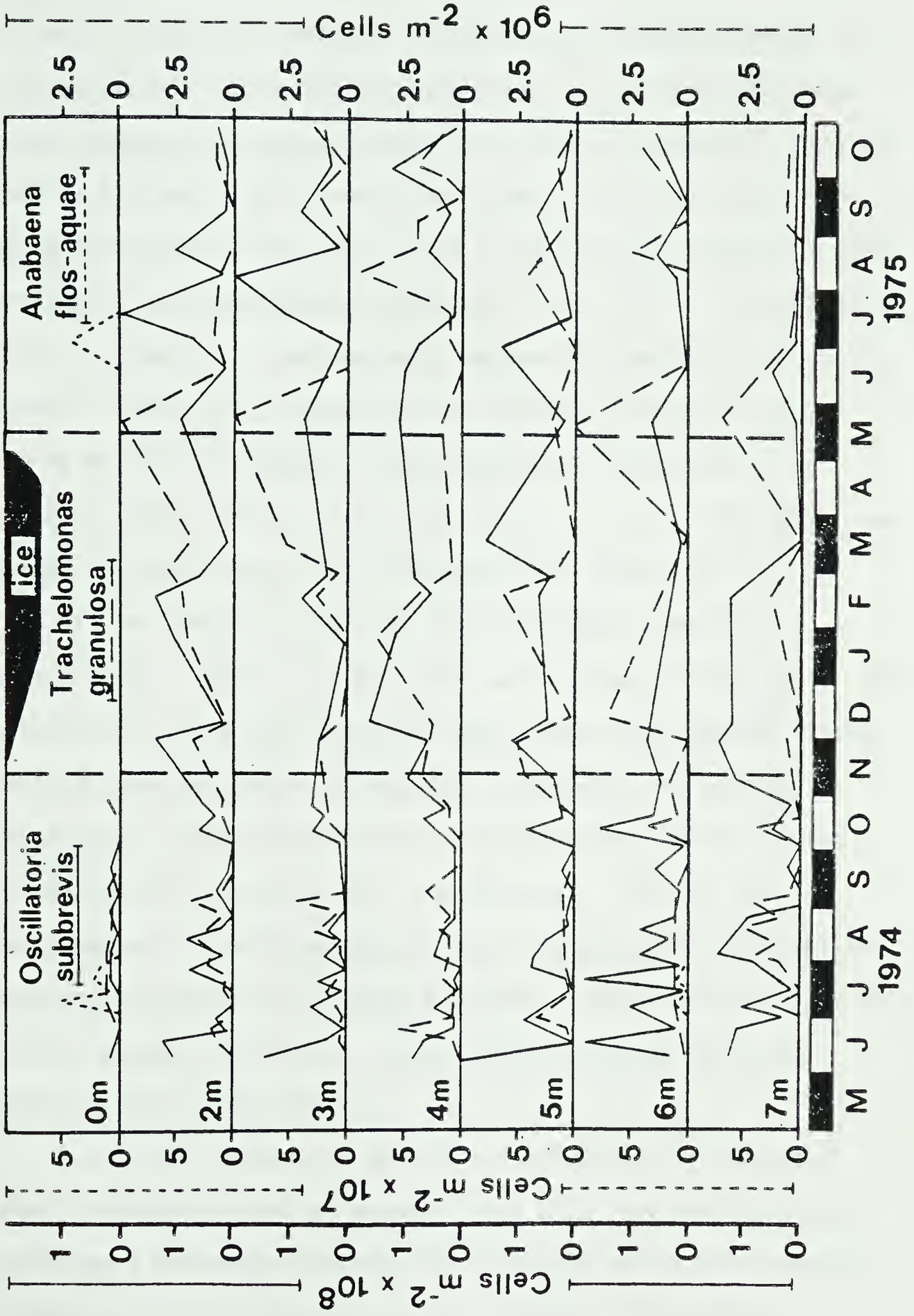

Cells m⁻² x 10⁷
Cells m⁻² x 10⁶
ice
13
10, 12
Nitzschia palea
Nitzschia gracilis
Achnanthes sp.
0m
2m
3m
4m
5m
6m
7m
M J J A S O N D J F M A M J J A S O
1974
1975

Figure 24.
Seasonal distribution depth by depth of
Oscillatoria subbrevis,
Trachelomonas granulosa,
and
Anabaena flos-aquae
for the epipelon.

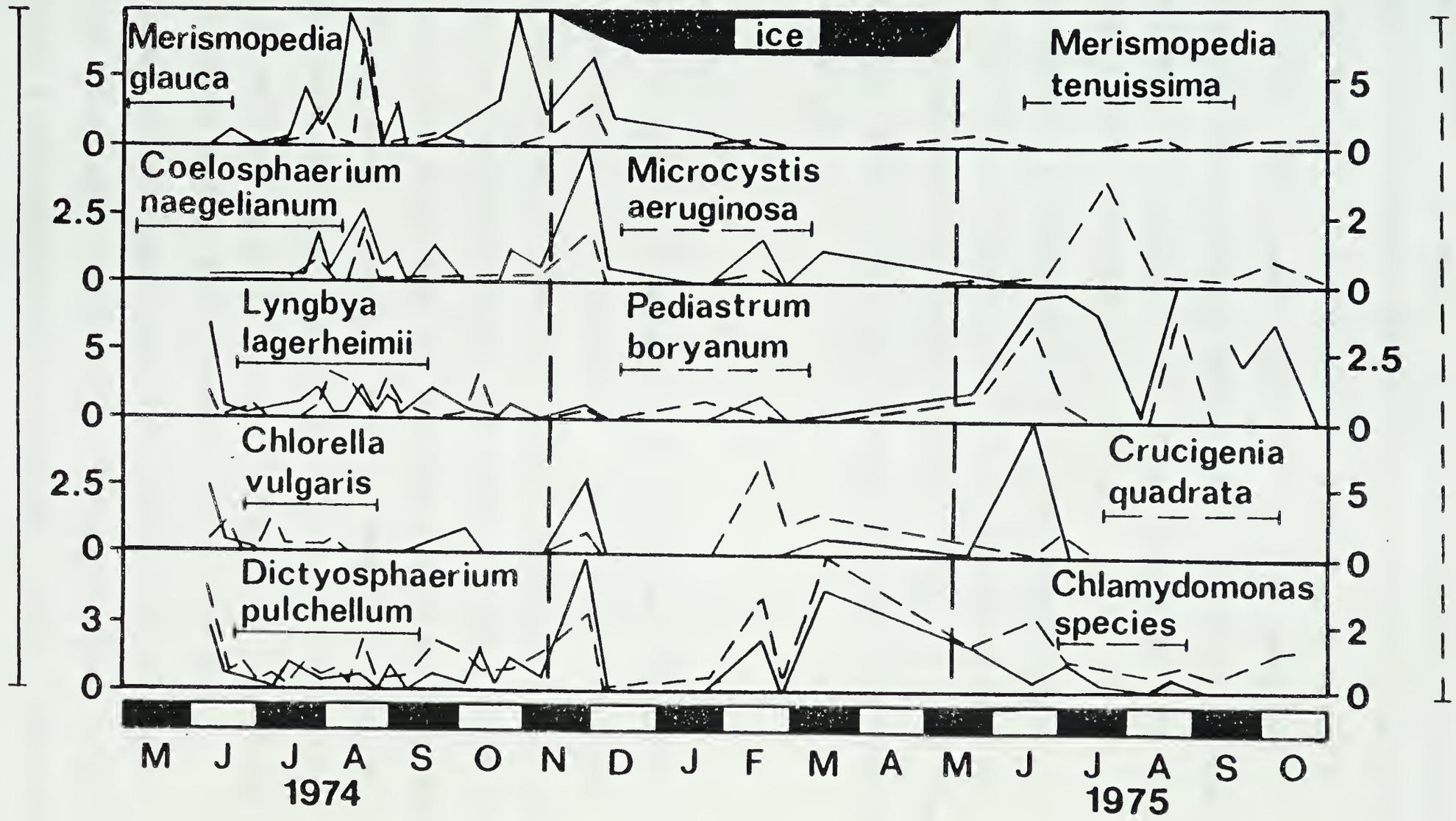

Oscillatoria subbrevis
ice
Trachelomonas granulosa
Anabaena flos-aquae
Cells m-2 x 10^6
Cells m-2 x 10^8
Cells m-2 x 10^7
0m
2m
3m
4m
5m
6m
7m
M J J A S O N D J F M A M J J A S O
1974
1975

blue-green showed the highest cell count of all dominants reaching 2.2×10^9 cells/ml in autumn. It grew best at sites 2 through 7 m, with large peaks occurring in every season. Another cyanophycean alga, Anabaena flos-aquae (Figure 24), reached a maximum in July at 0.25 m, and was rarely found at any other site except as akinetes, which were present year round. The final species to exhibit a depth preference was Trachelomonas granulosa (Figure 24). It grew best at sites 2 through 7 m, and reached a maximum in the late winter/early spring. Since light attenuation was extremely rapid, the algae living at sites 3 through 7 m were doing so at below the 1% irradiance level all year, while at site 2 m, only in the spring and autumn of each year did the irradiance level exceed 1%.

All the remaining dominant algae displayed no depth preferences; so, data from all sites were averaged (Figure 25). The cyanophycean algae Coelosphaerium naegelianum, Merismopedia glauca, Merismopedia tenuissima, Microcystis aeruginosa, and Lyngbya lagerheimii reached maxima during the summer and autumn with the latter species forming as well a spring peak. Finally, the chlorophycean algae Chlamydomonas spp., Dictyosphaerium pulchellum, Crucigenia quadrata and Chlorella vulgaris reached maxima during the spring, autumn, and winter, and Pediastrum boryanum exhibited activity in all four seasons.

Persistent patterns of vertical distribution for the major algal divisions present occurred (Figure 20). The Bacillariophyta exhibited a preference for the 0.25 m station, while the Cyanophyta showed a preference for the 2 to 7 m stations. Chlorophyta

Figure 25.
Seasonal distribution for mean of 7 depths
for
Merismopedia tenuissima,
Microcystis aeruginosa,
Merismopedia glauca,
Coelosphaerium naegelianum,
Lyngbya lagerheimii,
Pediastrum boryanum,
Chlorella vulgaris,
Crucigenia quadrata,
Dictyosphaerium pulchellum,
and
Chlamydomonas
spp.
in the epipelon.


Merismopedia glauca
ice
Merismopedia tenuissima
Coelosphaerium naegelianum
Microcystis aeruginosa
Lyngbya lagerheimii
Pediastrum boryanum
Chlorella vulgaris
Crucigenia quadrata
Dictyosphaerium pulchellum
Chlamydomonas species
5
0
2.5
0
5
0
2.5
0
3
0
5
0
2
0
2.5
0
5
0
2
0
M J J A S O N D J F M A M J J A S O
1974
1975

increased slightly with depth. The Euglenophyta tended to increase with depth. The cyanophytes dominated the cell counts (Figure 26). Only at the 0.25 m station were there consistently appreciable numbers of other algae, namely diatoms. The blue-greens were especially important during the summer and early winter. Diatoms and greens were best represented in spring, autumn, and late winter. Euglenophytes were most prominent in spring.

The composite representations of species composition as expressed by species diversity indices indicated that richness, evenness, and diversity decreased with depth (Figure 20), and showed high spring and summer values which decreased through the autumn and winter (Figure 27).

4.2.3. Standing Crop

The two standing crop measures, cell counts and chlorophyll *a*, did not always coincide (Hickman 1973). Taken together, however, they did indicate certain trends (Figure 28, Figure 29, Figure 30). During 1975, no consistent pattern with respect to depth occurred in standing crop size except that during February there was a decrease with increasing depth. Otherwise, patterns were quite irregular, with peaks often occurring at the deeper sites. Such irregular patterns occurred during 1976, but the utilization of fewer sampling depths eliminated some of this variation from site to site. Seasonal peaks did not always occur simultaneously at all depths (Figure 30). For example, during 1974 chlorophyll *a* peaks in June at 0.25 and 2 m preceded the much larger peaks in July at the lower

Figure 26.
Seasonal distribution of algal divisions expressed as $\log_{10}$ cell counts/m^2 (A) and as percent composition (B) for the epipelon.

T = total cells; Cy = Cyanophyta;
B = Bacillariophyta; Ch = Chlorophyta;
E = Euglenophyta.

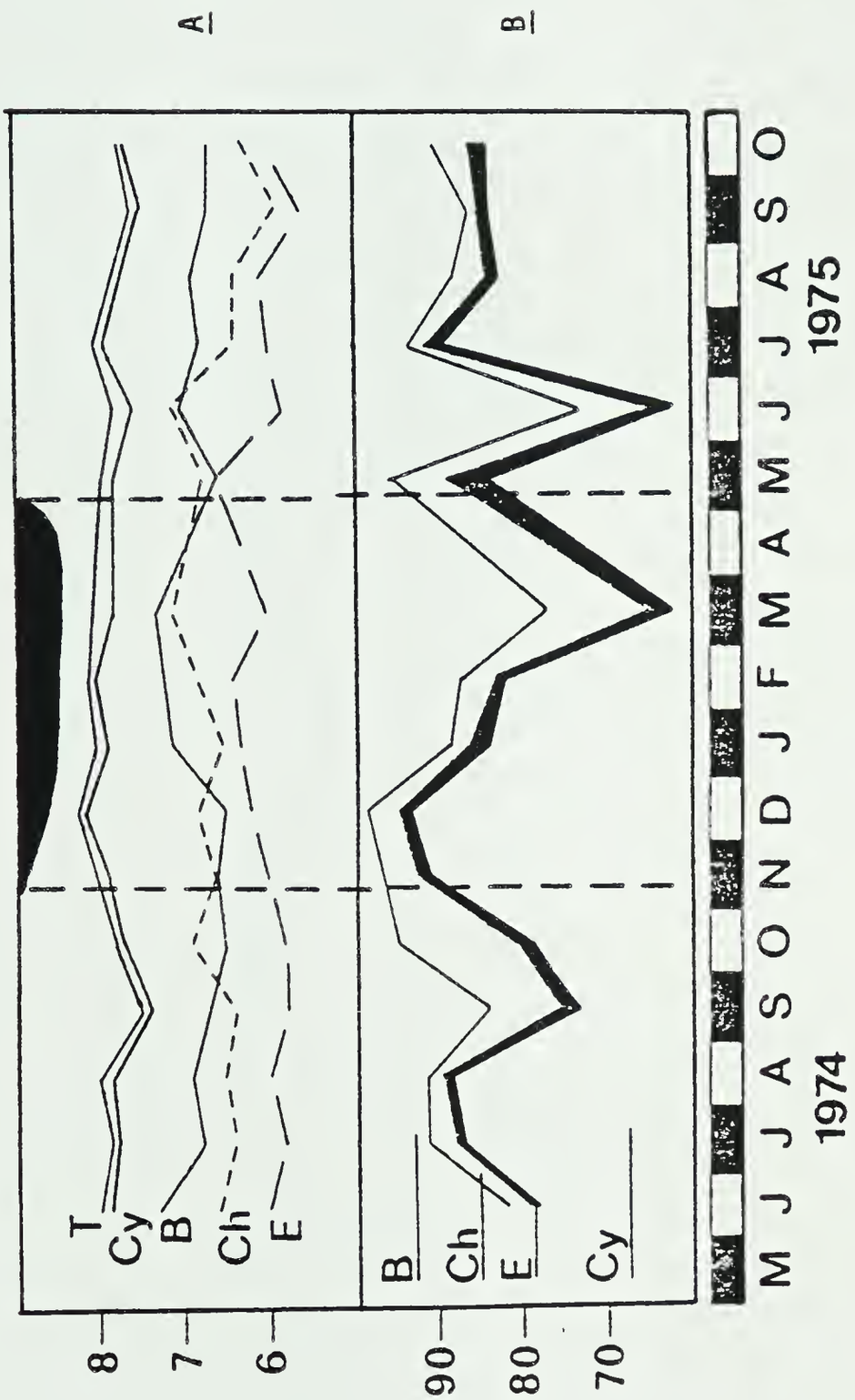

A
B
T
Cy
B
Ch
E
8
7
6
B
Ch
E
Cy
90
80
70
M J J A S O N D J F M A M J J A S O
1974
1975

Figure 27.
Seasonal distribution of number of species present, evenness, and Shannon's diversity for the epipelon.

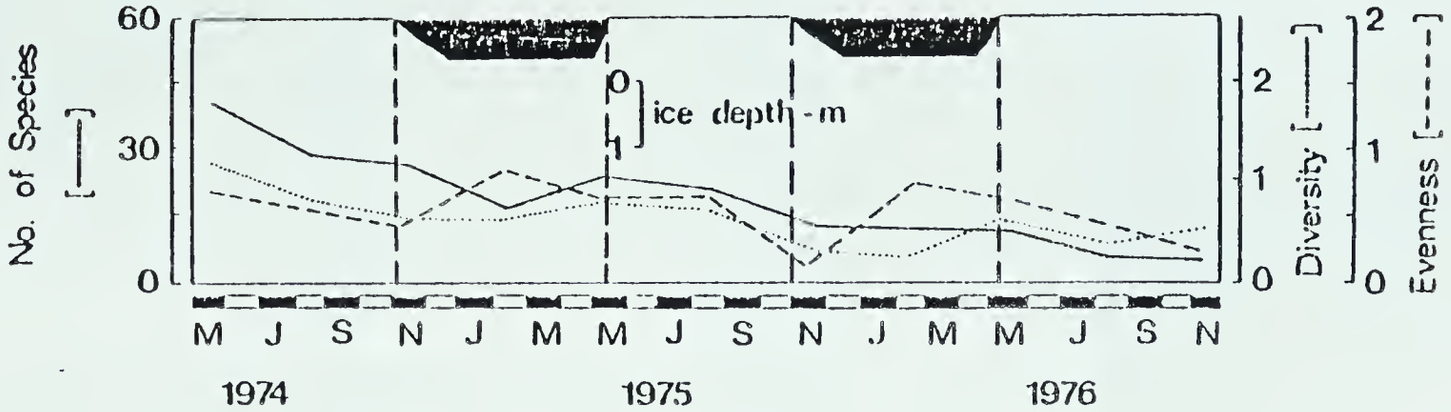

No. of Species [——]
60
30
0
0
1
ice depth - m
2
1
0
Diversity [——]
2
1
0
Evenness [- - - -]
M J S N J M M J S N J M M J S N
1974
1975
1976

Figure 28.
Vertical distribution of standing crop chlorophyll and cell counts for the epipelon.

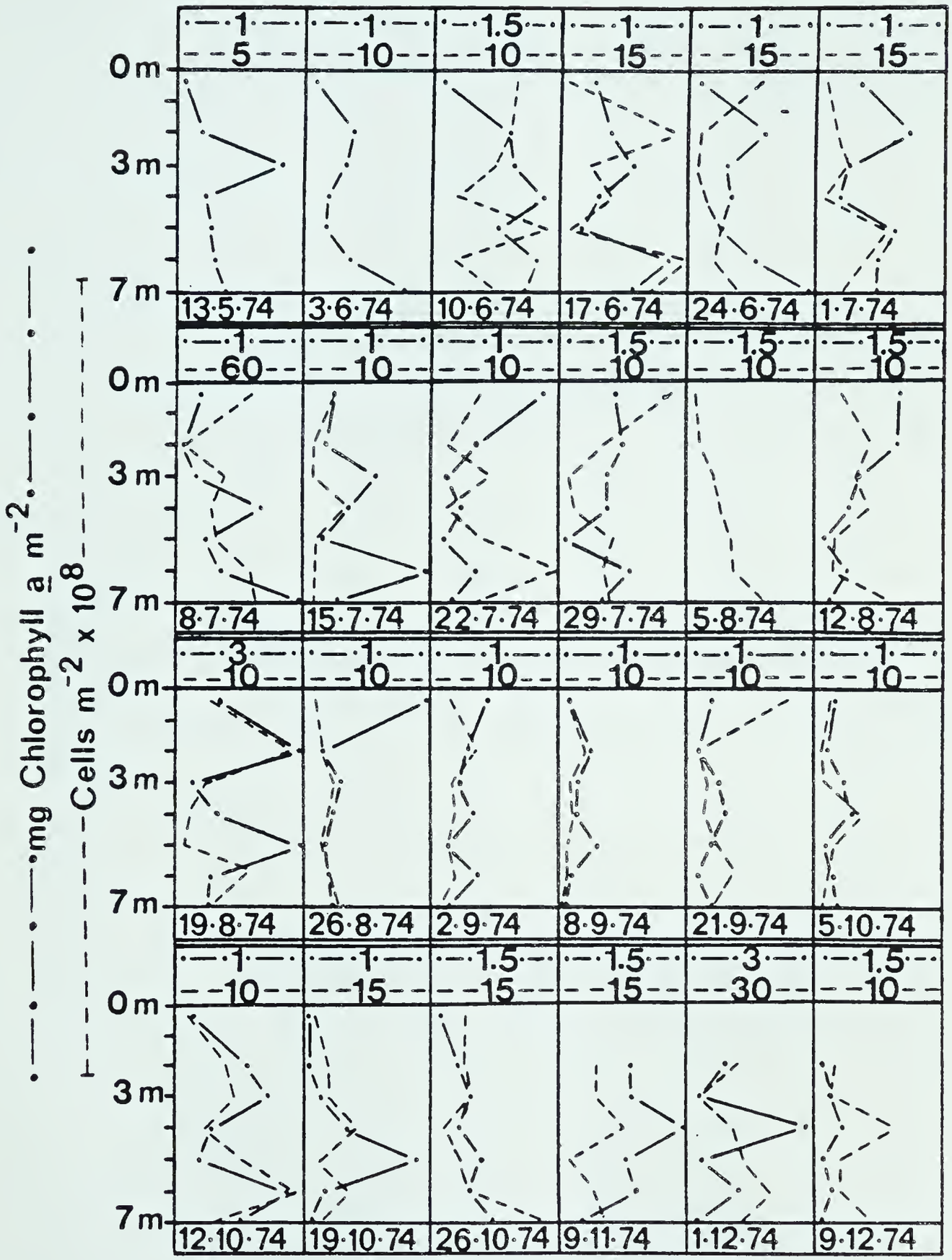

mg Chlorophyll a m-2
Cells m-2 x 10^8
0m
3m
7m
1 5
1 10
1.5 10
1 15
1 15
1 15
13·5·74
3·6·74
10·6·74
17·6·74
24·6·74
1·7·74
1 60
1 10
1 10
1.5 10
1.5 10
1.5 10
8·7·74
15·7·74
22·7·74
29·7·74
5·8·74
12·8·74
3 10
1 10
1 10
1 10
1 10
1 10
19·8·74
26·8·74
2·9·74
8·9·74
21·9·74
5·10·74
1 10
1 15
1.5 15
1.5 15
3 30
1.5 10
12·10·74
19·10·74
26·10·74
9·11·74
1·12·74
9·12·74

Figure 29.
Vertical distribution of standing crop chlorophyll, cell counts, and productivity for the epipelon.

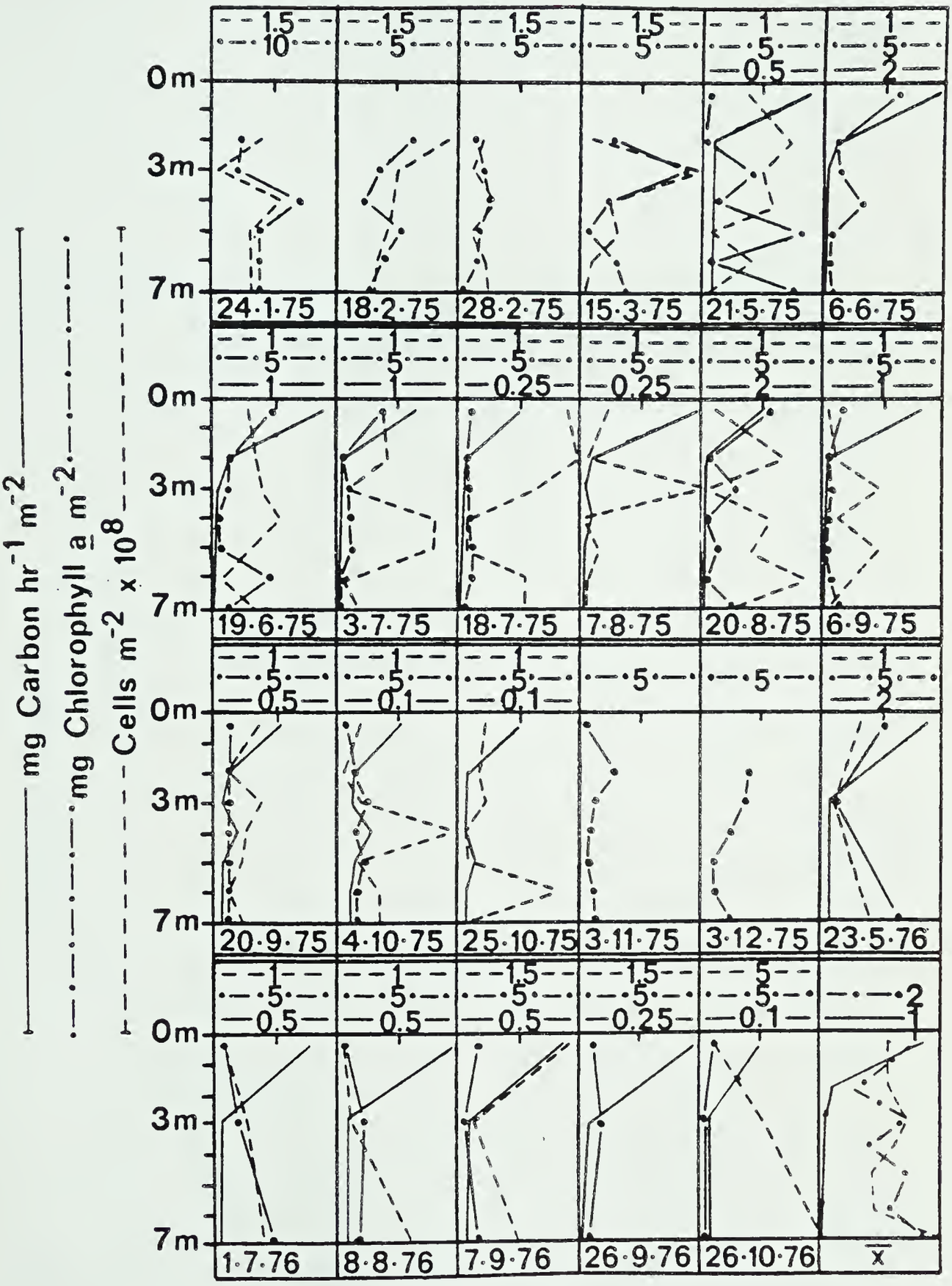
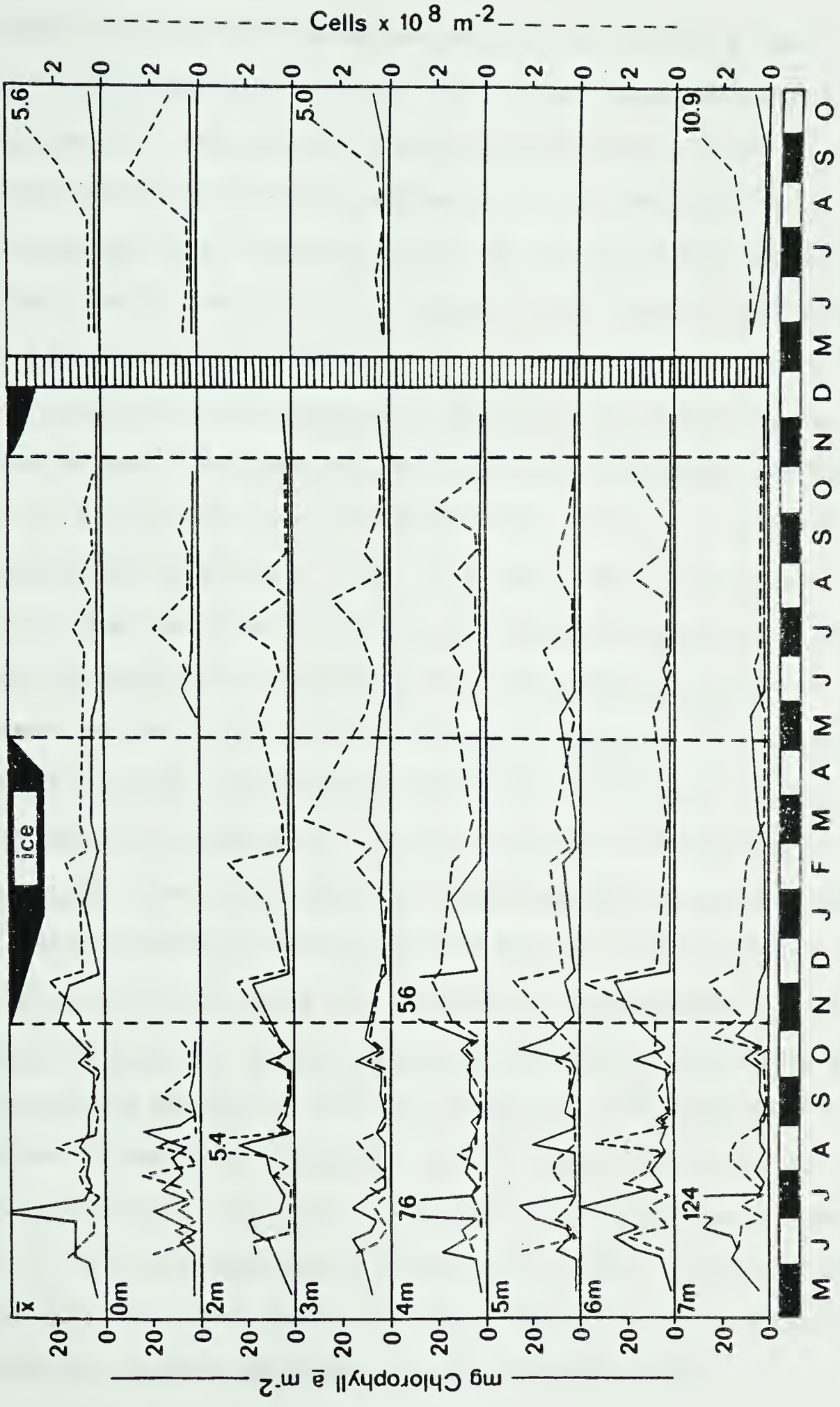

mg Carbon hr⁻¹ m⁻²
mg Chlorophyll a m⁻²
Cells m⁻² x 10⁸
0m
3m
7m
24·1·75
18·2·75
28·2·75
15·3·75
21·5·75
6·6·75
19·6·75
3·7·75
18·7·75
7·8·75
20·8·75
6·9·75
20·9·75
4·10·75
25·10·75
3·11·75
3·12·75
23·5·76
1·7·76
8·8·76
7·9·76
26·9·76
26·10·76
x̄

Figure 30.
Seasonal distribution depth by depth of standing crop chlorophyll and cell counts for the epipelon.


Cells x 10 8 m-2
mg Chlorophyll a m-2
ice
x̄
0m
2m
3m
4m
5m
6m
7m
5.6
5.4
5.0
56
76
124
10.9
M J J A S O N D J F M A M J J A S O N D M J J A S O
1974
1975
1976

depths. Most variability was associated with the 0.25 m site particularly during 1974 (Figure 30), and was undoubtedly due to wave action. This site was frozen during the winter, but significant standing crops continued at sites 2 through 7 m. Fluctuations at all depths were less in 1975 and 1976 as the mean total standing crop of 9.3 mg chlorophyll a/m^2 found in 1974 dropped to 1.6 and 1.8 mg/m^2 in 1975 and 1976, respectively.

Although the two measures of standing crop did not coincide depth by depth, the same seasonal trends were displayed. The mean of all stations served as an adequate representation of lakewide fluctuations (Figure 30). Total cell counts for 1974 produced a spring peak dominated by Navicula cryptocephala, Navicula gracilis, Navicula hungarica var. capitata and Oscillatoria subbrevis. A summer peak followed, dominated by Navicula hungarica var. capitata, Nitzschia palea, Coelosphaerium naegelianum, Merismopedia glauca, Merismopedia tenuissima, Microcystis aeruginosa and Oscillatoria subbrevis. The late autumn/early winter peak was dominated by the previously mentioned summer blue-green species. The mid-winter cell count standing crop peaks were dominated by Chlamydomonas species, Nitzschia gracilis, Nitzschia palea, Coelosphaerium naegelianum and Oscillatoria subbrevis. Total cell counts for 1975 repeated the pattern, though less distinctly, and 1976 counts showed only an autumn maximum. Chlorophyll a exhibited a spring maximum, a summer pulse and a late autumn/early winter peak in 1974. In 1975, values were low with spring, summer and late autumn/early winter activity dampened. In 1976, chlorophyll a values were again low.

4.2.4. Productivity

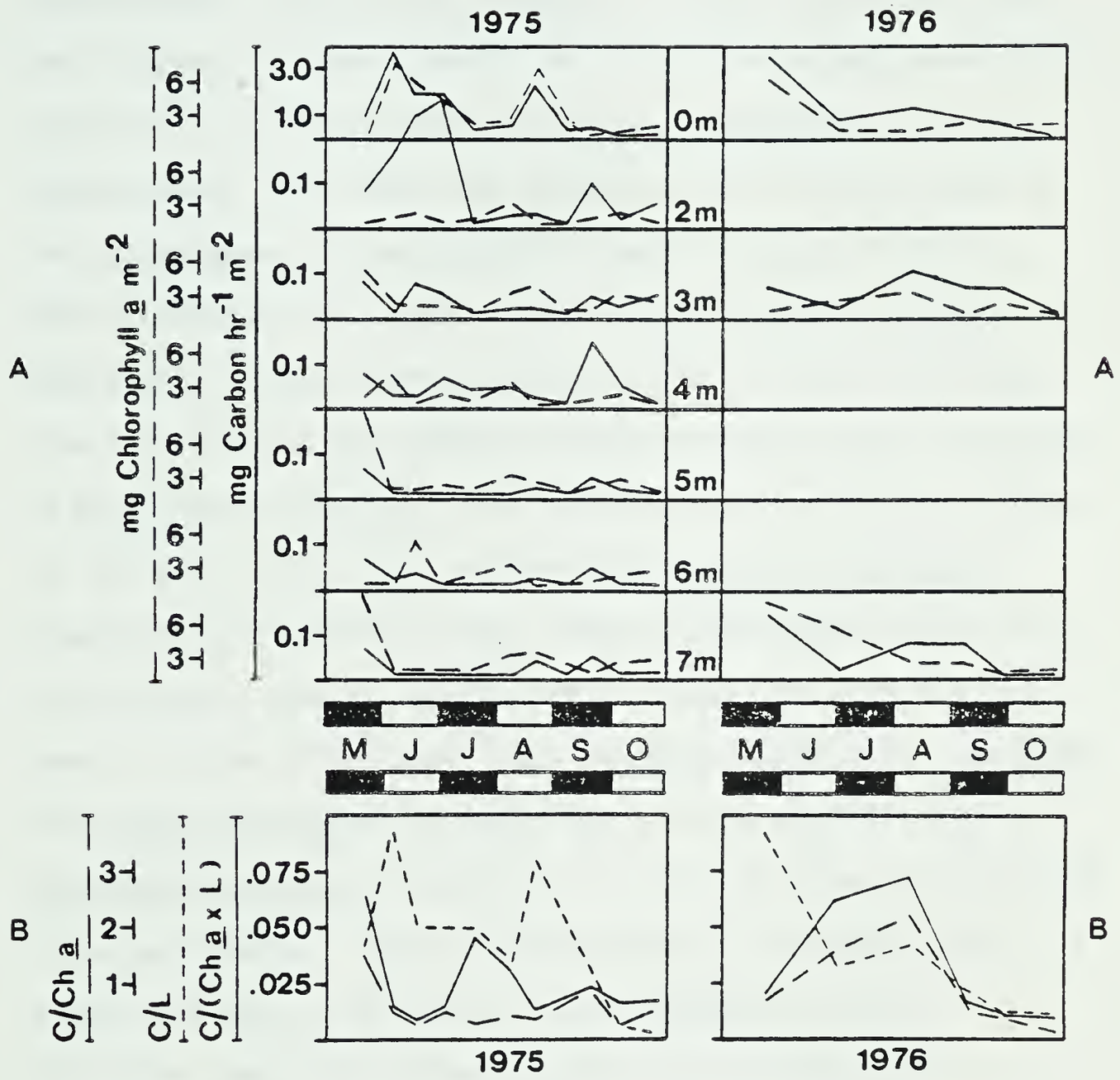
In contrast to standing crop, epipelic algal primary productivity was consistently greater at 0.25 m, and thereafter, decreased rapidly with increasing depth (Figure 29), hence decreasing light levels. For the May through October periods of 1975 and 1976, primary productivity at the 0.25 m site averaged 1.1 and 1.2 mg carbon/hr/m^2, respectively. At sites 2 through 7 m, it was 0.04 and 0.06 mg carbon/hr/m^2, respectively. On a total lake basis, 65% of the total epipelic algal productivity occurred within the 0 to 1 m depth interval, a region which comprises but 23% of the total lake area.

Seasonally, productivity followed chlorophyll _a_ closely (Figure 31). Seasonal fluctuations in productivity were similar depth by depth with spring, summer, and autumn peaks. During 1975, productivity at 0 m exhibited a spring peak of 3.7 mg carbon/hr/m^2 with diatoms dominating the cell counts; a late summer peak of 2.3 mg carbon/hr/m^2 occurred when blue-greens were the major dominants; and an autumn peak of 1.0 mg carbon/hr/m^2 was co-dominated by blue-greens and diatoms. The results for the ice free period of 1976 were similar to those of 1975, but with a less pronounced summer peak. Expressed on a total lake basis, 7.1×10^3 kg carbon was produced May through October of 1975 and 8.0×10^3 kg carbon in 1976.

4.2.5. Cross Incubation Studies

The relative photosynthetic capabilities of epipelic algae from

Figure 31.
Seasonal distribution depth by depth of mg chlorophyll a/m^2 and mg carbon/hr/m^2 (A). Seasonal distribution of the photosynthetic index C/Ch a, photosynthetic efficiency C/L, and productivity efficiency C/(Ch a x L) based on 0 m data (B) for the epipelon.


1975
1976
A
A
mg Chlorophyll a m-2
mg Carbon hr-1 m-2
6
3
3.0
1.0
0.1
0m
2m
3m
4m
5m
6m
7m
M J J A S O
M J J A S O
B
B
C/Ch a
C/L
C/(Ch a x L)
3
2
1
.075
.050
.025
1975
1976

0.25, 3, and 7 m sites were assessed in 1976 with cross incubation studies (Figure 32, Figure 33). In all experiments, samples from each collection depth showed higher productivity values and photosynthetic indices when incubated at higher suspension depths, hence higher irradiance levels. On 23 May, the highest productivity occurred at 0.25 m dominated by Navicula cryptocephala, and the photosynthetic index there was comparable with a maximum shown by the Chlamydomonas dominated sample from 3 m at every incubation depth (Figure 32, Figure 33). At 7 m, Oscillatoria subbrevis dominated this least active collection, but by 1 July, the sample from 7 m possessed the highest productivity and was still dominated by Oscillatoria subbrevis. The photosynthetic indices were highest for the 0.25 m site, again dominated by Navicula cryptocephala. Productivity differences in the remaining experiments did not vary conspicuously; however, photosynthetic indices did. On 7 August, a sample from the 0.25 m site, where Navicula hungarica var. capitata and Lyngbya lagerheimii co-dominated, gave the highest indices. Oscillatoria subbrevis dominated all collection depths for the last three experiments. The prominent indices on 6 September were produced by the 3 m collection, on 25 September by the 7 m collection, and on 27 October by the 3 and 7 m collections.

4.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

Results from the three productivity relationships have been tabulated (Table 6). The mean photosynthetic index decreased with

Figure 32.
Productivity for the epipelon expressed as a function of collection and incubation depths.

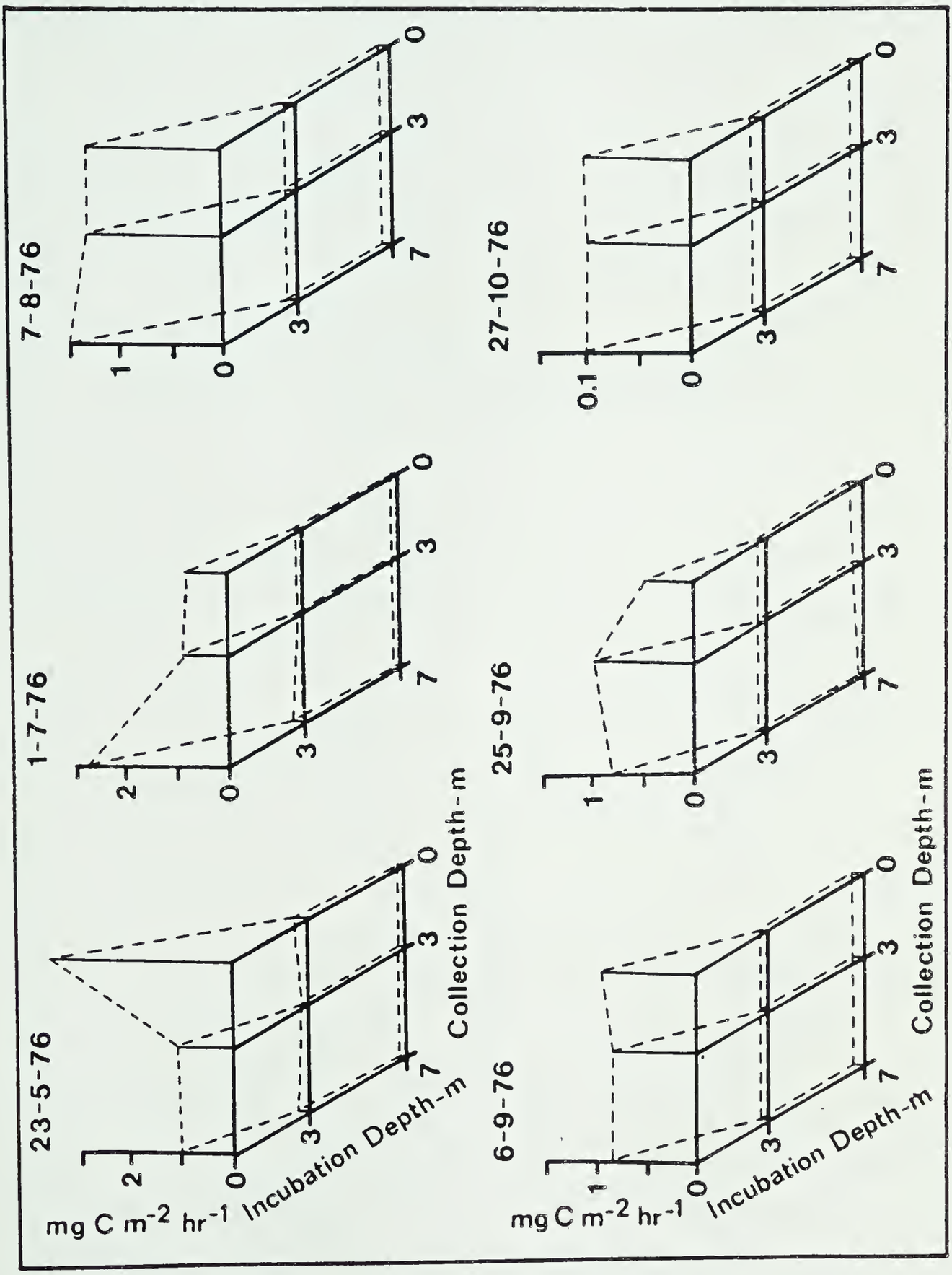

7-8-76
27-10-76
1-7-76
25-9-76
23-5-76
6-9-76
mg C m-2 hr-1
Incubation Depth-m
Collection Depth-m

Figure 33.
Photosynthetic index for the epipelon expressed as a function of collection and incubation depths.

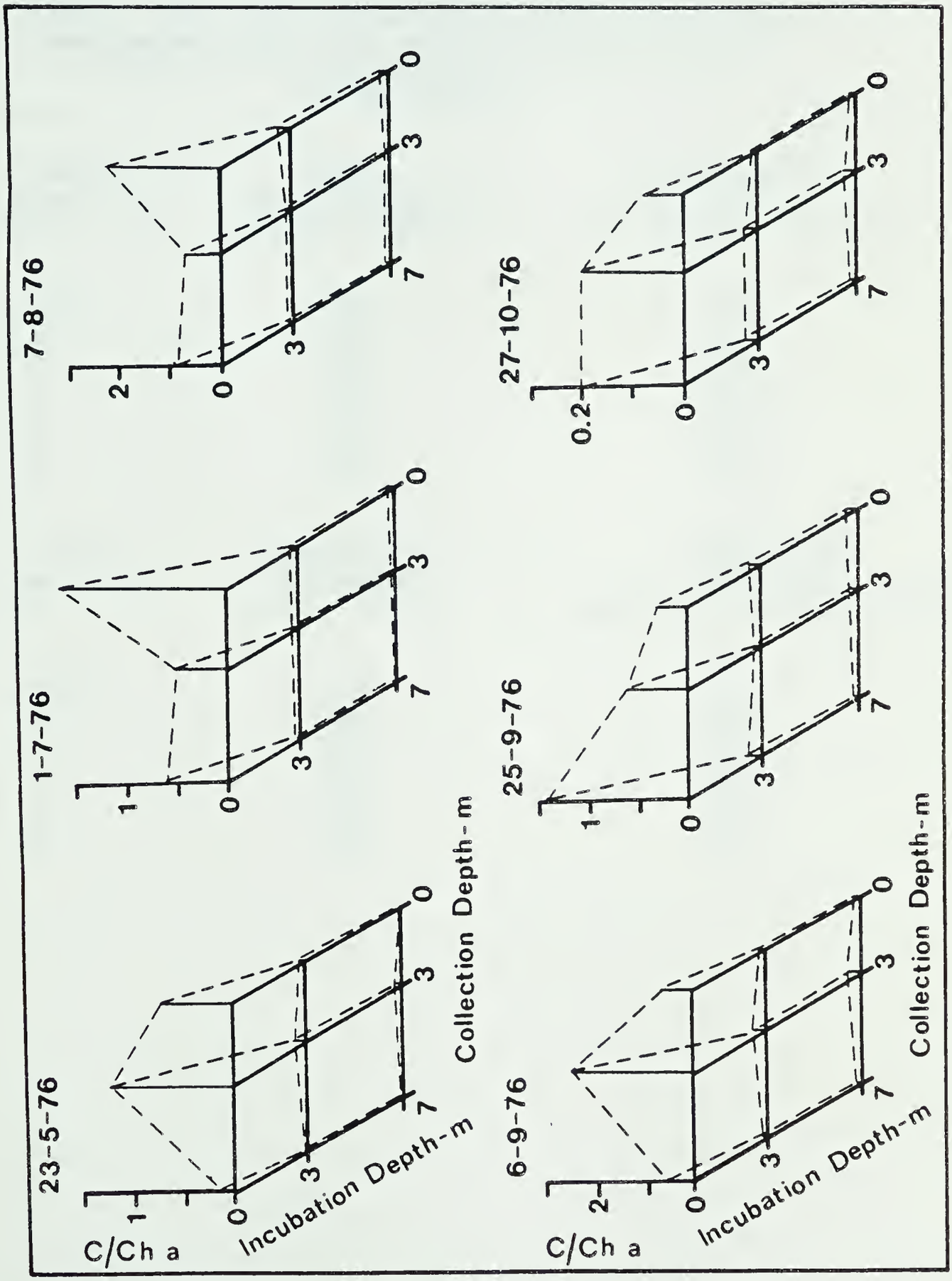

23-5-76
1-7-76
7-8-76
6-9-76
25-9-76
27-10-76
C/Ch a
Incubation Depth-m
Collection Depth-m
0
3
7
1
2
0.2

Table 6. Mean primary productivity, photosynthetic index, photosynthetic efficiency, and productivity efficiency during the May through October period of 1975 for the epipelon.

Site (depth in m)	Mean Primary Productivity mg C h^{-1} m^{-2}	Photosynthetic Index mg C (mg chloro'a)$^{-1}$ h^{-1}
0.25	1.06	0.51
2	0.10	0.12
3	0.04	0.02
4	0.05	0.04
5	0.02	0.01
6	0.02	0.02
7	0.02	0.01

Site (depth in m)	Photosynthetic Efficiency mg C h^{-1} m^{-2} I^{-1}	Productivity Efficiency mg C (mg chloro'a)$^{-1}$ h^{-1} I^{-1}
0.25	0.03	0.02
2	0.25	0.46
3	0.33	0.21
4	0.50	0.50
5	0.55	0.67
6	0.65	0.73
7	0.69	0.41

increasing depth quickly at first, but then was low and somewhat variable. In contrast, the photosynthetic and productivity efficiencies generally increased with depth (Table 6) which demonstrated the increased efficiency of epipelic algae at lower irradiance levels. Data from the 0.25 m site which represented maximum epipelic algal productivity were used to present these relationships on a seasonal basis (Figure 31). For all, a spring maximum preceded lesser summer peaks.

4.3. Discussion

4.3.1. Physico-chemical Parameters

The Hastings epipelon is characterized by the vertical distribution of light and sediments into two distinct habitats. The first is the 0 to 2 m region which lies within the euphotic zone and has sandy podzolic sediments. The second is the 2 to 7 m region which lies within the aphotic zone and has sediments of gyttja that approach 50% organic content.

Other physico-chemical parameters, though of note, were not considered as important overall. Water temperatures near the sediments were made somewhat less rigorous by the overlying water and the sediments themselves; yet the relatively rapid spring heating and autumn cooling characteristic of lakes in the prairie-parkland (Klarer and Hickman 1975, Hickman 1978, 1979a,b,c) was noted. Dissolved oxygen was quite low (< 5%) whenever algal photosynthesis was low, for example in winter, and whenever large amounts of organic material were decomposing, for example in winter

and early summer. Although pH values did not fluctuate greatly, a pattern similar to that for oxygen was seen with low values when photosynthesis was low and/or decomposition was high. Bicarbonate (carbon), silica, nitrate, and orthophosphate followed patterns more or less common in eutrophic temperate lakes (3.3.1. Physico-chemical Parameters, Wetzel 1975). The chemical interactions among the sediment, the sediment microzone layer, and the overlying water was evident (Mortimer 1941, 1942, 1972). Changes in seasonal contributions from the sediment were only indirectly evaluated through changes in the chemistry of the overlying water. The difficulty of assessing the seasonal influence of sediment chemistry as it applies directly to epipelic algae remains a problem.

4.3.2. Species

The major dominants found most in the higher light 0 to 2 m region of sandy podzolic sediments were diatoms. Two of the dominant diatom species at 0.25 m were Navicula cryptocephala and Navicula gracilis. Navicula cryptocephala has been recorded in a wide spectrum of conditions (Hustedt 1930, Round 1956, 1957a,b,c, 1972, Hickman 1974, 1975, 1976b, 1978, Hickman and Round 1970), and the possibility of phenotypic adaptations to various habitats exists (Eaton 1967).

In Hastings epipelon, the species was most strongly associated with light ($r = 0.740$, $p < 0.05$), and showed a negative correlation with major nutrients, most notably silica ($r = -0.540$, $p < 0.10$).

Navicula gracilis also showed an association with light ($r = 0.640$, $p < 0.05$), but only weak, nonsignificant, negative correlations with nutrients.

The other two dominant diatoms at the 0.25 m station, Navicula hungarica var. capitata and Achnanthes spp., have been associated with sandy sediments (Round 1965, Eaton 1967, Hickman and Round 1970), but both have been found widely tolerant of various conditions (Hustedt 1930, Round 1957b, Round 1972, Hickman 1976b). It is suggested that the sandy texture of the Hastings sediment was influential upon species composition since these two species, as well as Opephora martyi Herib, a common epipsammic species (Round 1965, Hickman and Round 1970), increased in Hastings as the proportion of sand in the sediment increased due to shore erosion aggravated by an adjacent road. However, these two species also showed a strong positive correlation with light and negative correlations with nutrients. For Navicula hungarica var. capitata the correlation with light was greatest ($r = 0.820$, $p < 0.05$) followed by the correlation with silica ($r = -0.680$, $p < 0.05$). For Achnanthes spp., the correlation with silica was greatest ($r = -0.590$, $p < 0.10$), followed by light ($r = 0.440$, $p < 0.10$).

The blue-green alga Anabaena flos-aquae was likewise most often found at 0.25 m. It also displayed a strong correlation with light ($r = 0.460$, $p < 0.10$) with weak, nonsignificant, negative correlations with nutrients. More importantly, it occurred in the phytoplankton in "bloom" proportions, where it floated to the surface and collected along shorelines. There it senesced and

settled out onto the sediment, thus accounting for its spatial and temporal distribution in the epipelon. The seasonal patterns of populations from the epipelon and the phytoplankton correlated closely ($r = 0.990$, $p < 0.05$).

In contrast to those dominants from 0.25 m, the dominants at sites 2 through 7 m showed negative correlations with light and positive correlations with nutrients. Indeed, species at 2 through 7 m had to contend with light below the 1% level and organic sediments. The dominants at these deeper sites consisted of the blue-green Oscillatoria subbrevis, the euglenophyte Trachelomonas granulosa, and the two diatoms Nitzschia palea and Nitzschia gracilis.

Oscillatoria species are often reported as important members of the epipelon (Round 1957c, Gruendling 1971, Kowalczewski, et al. 1973, Moore 1974a,b, Kairesalo 1977, Hickman 1978). In Hastings epipelon, Oscillatoria subbrevis exhibited a positive correlation with nutrients, most notably bicarbonate ($r = 0.500$, $p < 0.10$), and a negative correlation with light ($r = -0.320$, $p < 0.25$). This species was especially interesting in that it showed population peaks in all four seasons. Trachelomonas granulosa was more restricted in that it peaked only in winter, but it too showed a positive correlation with bicarbonate ($r = 0.520$, $p < 0.10$) and a negative correlation with light ($r = -0.750$, $p < 0.05$). In addition, there was a strong positive correlation with silica ($r = 0.760$, $p < 0.05$).

Nitzschia palea is recognized as a widespread species and is

seen as having a distinct preference for high nutrient levels, especially nitrogen (Round 1957b, Archibald 1972, Hickman 1975, Moore 1977). In Hastings, it did show strong positive correlations with all four major nutrients monitored, that is, orthophosphate ($r = 0.950$, $p < 0.05$), silica ($r = 0.840$, $p < 0.05$), bicarbonate ($r = 0.820$, $p < 0.10$), and nitrate ($r = 0.700$, $p < 0.10$). Also, there was a negative correlation with light ($r = -0.570$, $p < 0.10$). Similarly, Nitzschia gracilis possessed positive correlations with nutrients; especially strong bicarbonate ($r = 0.670$, $p < 0.10$) and orthophosphate ($r = 0.610$, $p < 0.10$) coefficients were noted. A negative, but weak, nonsignificant correlation existed against light.

The broad tolerance limits of each of the four aforementioned species have been reported in other studies (Round 1972, Moore 1974a, Hickman 1976b, Kairesalo 1980). Moss (1969b) found a blue-green Arthrospira species, a euglenophyte Trachelomonas species, and a diatom Nitzschia species under similar low light and organic sediment conditions. These stress tolerant species tend to become dominants in the absence of less tolerant competitors (Odum 1971).

Other dominant species displayed no depth preferences, but instead exhibited broader light level tolerances, and were competitive in the 0 to 2 m as well as the 2 to 7 m regions. However, they tended to be less frequent dominants. Among the blue-greens in the group, Lyngbya species, Merismopedia glauca, Merismopedia tenuissima, Coelosphaerium naegelianum, and Microcystis

aeruginosa have been recorded on the epipelon in other studies (Round 1957c, Moore 1974b, Stanley 1976a, Kairesalo 1977, Hickman 1978). In Hastings, Lyngbya lagerheimii, Merismopedia glauca, and Merismopedia tenuissima were most closely correlated with temperature ($r = 0.610$, $p < 0.10$; $r = 0.550$, $p < 0.10$; $r = 0.340$, $p < 0.25$, respectively) with similar, though weaker correlations with light and weaker negative correlations with nutrients. Somewhat in contrast, Coelosphaerium naegelianum in Hastings showed a negative correlation against temperature ($r = -0.360$, $p < 0.25$) with a weaker, nonsignificant, negative correlation against light and weak, nonsignificant, positive coefficients against nutrients. Microcystis aeruginosa populations did not show any significant correlations with physico-chemical parameters monitored, and no obvious association existed between epipelic and phytoplanktonic populations. However, data from cross incubation studies indicate Microcystis aeruginosa and Coelosphaerium naegelianum populations in the epipelon during winter were actually senescing phytoplankton populations (3.1.5. Cross Incubation Studies, 4.1.5. Cross Incubation Studies).

The chlorophycean dominants not associated with depth preferences likewise were dominants infrequently. They were commonly found in the phytoplankton and tended to be linked seasonally to the nutrient status of the overlying water. For example, Chlamydomonas spp., Crucigenia quadrata, and Dictyosphaerium pulchellum increased during periods of high nutrient concentrations, most notably nitrate was noted for the first species

($r = 0.920$, $p < 0.05$), orthophosphate for the second species ($r = 0.700$, $p < 0.10$), and nitrate for the third species ($r = 0.880$, $p < 0.05$). In contrast, Chlorella vulgaris increased when nutrients were low, especially silica ($r = -0.490$, $p < 0.25$), and Pediastrum boryanum increased when many of the nutrients were low, especially the bicarbonate ($r = -0.610$, $p < 0.10$).

All dominant algal species are thought to develop under particular conditions circumscribed by seasonal shock periods (Round 1971). In the phytoplankton, dominants rarely survive such shock periods and readapt to the following set of environmental conditions, but in the epipelon, the relatively stable habitat can buffer changes, and persistent dominants may reoccur (Round 1964, 1972). Such appears to have been the situation for the epipelon of Hastings Lake as five of the dominant species displayed dominance in at least three of the four seasons, and Oscillatoria was a dominant in all four seasons.

Algal divisions based on morphological and physiological differences should express those differences in spatial and temporal preferences. A range of physical and chemical parameters should be recognizable. Such indeed is the case for the phytoplankton (Hutchinson 1967).

Vertical distributions of algal divisions on the epipelon have been reported. Round (1961b) reported maximum diatom populations at shallow stations with blue-greens decreasing evenly with depth in two eutrophic English lakes. Moss (1969b) found diatoms most numerous at shallow stations with flagellates and blue-greens most

abundant at deeper sites in Abbot's Pond, England. Gruendling (1971) found blue-greens most abundant at shallow stations with diatoms equally frequent at shallow and intermediate depths, while greens were most abundant at the intermediate depths in a shallow, low nutrient lake in British Columbia. Kairesalo (1977) reported that over a 4 m depth range in Lake Paajarvi, diatoms increased with depth, greens decreased with depth, and blue-greens maintained even populations through 3 m with a decrease at 4 m. Contrastingly, in five eutrophic prairie-parkland lakes near Hastings Lake, little floristic difference was found between shallow and deep sites by Hickman (1978).

At the Hastings 0 m station, there were higher light levels and lower organic content for the sediments, representing moderate conditions compared to the 2 to 7 m depths. At 0 m in Hastings, diatoms were successful in competing with the other algae for space and nutrients. At 2 to 7 m stations in Hastings, blue-greens were dominant, perhaps because of their ability to remain active at extremely low light levels and their preference for highly organic sediments. Specific chromatic and heterotrophic adaptions of blue-greens have been noted by other authors (Round 1964, Van Baalen, et al. 1971, Kairesalo 1976). Moss (1969b) associated "polluted" waters with increasing depth and found blue-greens important there.

Hastings chlorophytes and euglenophytes showed a similar, though less pronounced trend. There was a preference to the higher organic content at 2 to 7 m stations (Round 1957a, Pamatmat 1968).

Since the seasonal patterns of abundance for the major algal divisions are usually associated with the "seasons", one might expect light and temperature, as the two most obvious manifestations of temperate seasonallity, to closely relate to algal patterns. The seasonal aspect of chemical parameters is not always so clear, and when attempting to establish associations between the epipelon and water chemistry, one must be aware of the problems posed by potential nutrient availability from the sediments (Round 1957a). Most authors suggest temperature and light as the major controlling factors of seasonallity.

Round (1960) proposed a seasonal pattern for epipelic diatoms of low winter, high spring, variable summer, and moderate autumn populations. Studies by Moss (1969a), Hickman and Round (1970), Gruendling (1971), Kairesalo (1977), and the present study have shown this pattern in a variety of lakes. Although the Chlorophyta was never a major group on Hastings epipelon, it was most important in the spring, autumn, and winter. This is contrary to Kairesalo (1977) and Hickman (1978), both of whom found green algal peaks with summer high temperatures. Gruendling (1971) and Kairesalo (1977) have also cited summer temperatures (15 to 20 °C) as the stimulating factor for epipelic blue-green seasonallity. However, Hastings cyanophytes were equally important in summer and winter.

The seasonal trends of the algal divisions in Hastings indicate a correspondence with light and temperature. However, relationships with nutrient cycles cannot be ruled out. As Round (1957a), Gruendling (1971), Moss (1969b) and Hickman (1978) have suggested,

orderly changes in species composition along physical, chemical, and temporal gradients exist. Differences of lake morphology, trophy, species composition, and the interrelationships among communities provide a variety of circumstances in the studies cited.

Diversity indices, used as quantitative measures of total species activity, decreased with increasing depth, hence increasing stress through rapid light attenuation. Seasonally, these indices tended to be higher in spring with values thereafter declining. Increasing irradiance and temperature, and newly circulated nutrients produced a favorable environment for many species in spring. As the growing season progressed, the community was stressed more and more. Physico-chemical changes coupled with biotic competition began to favor those species more tolerant of adverse conditions. By winter, only a few species persisted under high stress.

4.3.3. Standing Crop

Epipelic standing crop may decrease with increasing depth, that is, as light decreases (Moss 1967a, 1969a,b, Gruendling 1971, Hickman 1971a). However, in Hastings Lake the standing crop varied irregularly with depth, while mean values changed little from shallow to deeper sites. Round (1961b, 1964) suggested grazing, biotic heterogeneity, and substrate variation, could cause considerable irregularities. Standing crop in the shallow water around the shore could easily have been reduced by wave action; whereas, the long term accrual of standing crop through efficient

photosynthesis at low light levels, or through heterotrophy, could have occurred in the relative physical stability of the deeper water sites.

Reports on seasonal patterns of epipelic standing crop vary greatly (Round 1960, 1964, Pamatmat 1968, Hickman and Round 1970, Gruendling 1971, Cadee and Hegeman 1974). Hickman (1978) showed a tendency toward a summer maximum in a study of five prairie-parkland lakes, reminiscent of Round's (1955) comments on the epipelon of ponds. Hastings Lake epipelon likewise showed this tendency.

Suggested factors affecting the temporal distribution of epipelic standing crop include grazing, phytoplankton shading, temperature, light, and the nutrient status of the overlying water (Round 1968, Moss 1969a, Hargrave 1970, Hickman 1978). The epipelon has been recognized as a potentially concentrated food source for animals (Marshall 1970, Hickman 1971a, Fenchel 1975, Stanley 1976b), and grazing activity can have decided positive and negative effects on epipelic standing crop size (Brook 1955, Eaton 1967, Hickman and Round 1970, Hargrave 1970). Data from the Hastings plankton suggest zooplankton populations affect the phytoplankton (Baker 1977), thus the potential affect exists for the epipelon. More definite is the interplay of Hastings phytoplankton standing crop and that of the epipelon during the ice free seasons; as one increases the other decreases.

Yet no single overriding factor controlled Hastings epipelic standing crop. Incident light, temperature, and the nutrient status of the overlying water are associated with standing crop

fluctuations also. The complexity of the situation can be illustrated as positive, though low and not significant, correlations existed for standing crop chlorophyll *a* against light and temperature, but negative significant correlations of standing crop cell counts were shown against the same two parameters ($r = -0.510$, $p < 0.10$; $r = -0.450$, $p < 0.25$, respectively). Then, too, Hickman (1978) makes the point that in shallow eutrophic prairie-parkland lakes, epipelic standing crop is more closely related to seasonal nutrient levels than has been found the case in studies from other lakes. In Hastings, standing crop chlorophyll *a* did show negative correlations with nutrients, most substantially nitrate ($r = -0.390$, $p < 0.25$), while standing crop cell counts showed positive correlations, most notably bicarbonate ($r = 0.550$, $p < 0.10$).

4.3.4. Productivity

Studies relating epipelic productivity to the depth of the overlying water have been based on the assumption that light is a major controlling factor (Gruendling 1971, Hickman 1971a, Gargas 1972). Indeed, for the Hastings epipelon this seemed to be the case, with both productivity and light decreasing markedly with depth.

Seasonal patterns of epipelic algal productivity vary, but light and temperature have often been cited as the major controlling factors (Round 1955, Grontved 1960, 1962, Pamatmat 1968, Hargrave 1969, Gargas 1970, Leach 1970, Gruendling 1971, Hickman 1971a,

Hunding 1971, Hunding and Hargrave 1973, Cadee and Hegeman 1974, Stanley 1976a, Kairesalo 1977, 1980). The only other determinant regularly cited is standing crop size, particularly as measured by chlorophyll a content (Hickman and Round 1970, Leach 1970, Gruendling 1971, Hickman 1971a,b, Cadee and Hegeman 1974, 1977, Stanley and Daley 1976, Kairesalo 1977). Epipelic algal productivity in Hastings Lake was closely correlated with both light level (1975, $r = 0.850$, $p < 0.05$; 1976, $r = 0.940$, $p < 0.01$) and also the chlorophyll a values (1975, $r = 0.930$, $p < 0.05$; 1976, $r = 0.880$, $p < 0.05$).

Yet other factors undoubtedly influence epipelic productivity. Grazing may depress, or stimulate, activity (Hargrave 1970, Fenchel 1975). Nutrient changes and biotic interrelationships within and among algal communities may have direct bearing on the state of any particular community. Changes in community productivity can result as communities overlap varying photosynthetic capabilities.

4.3.5. Cross Incubation Studies

Cross incubation studies evaluated the photosynthetic capabilities of epipelic populations crossing site and shock period boundaries.

Within the range of chlorophyll a values investigated, similar productivity values tended to occur at given light levels, regardless of chlorophyll a quantity. The photosynthetic index patterns revealed populations at 0 and 3 m sites possessed greater photosynthetic potential during the first half of the ice free

season when light levels, temperature, and nutrients were higher. The 3 to 7 m populations showed greater potential as environmental stress increased during the latter half of the ice free season.

4.3.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

The photosynthetic index relating productivity to standing crop chlorophyll a provided information on the quality of photosynthetic activity (Fogg 1963, Hickman 1976a). Hastings values from the epipelon were comparable to those garnered from studies of other algal communities (Ryther and Yentsch 1957, Odum 1971). The index was highest in spring with a mid-summer decrease and a subsequent late summer/early autumn pulse rounding out a general decline into autumn; much the same pattern was reported by Cadee and Hegeman (1974). The dependence of this index upon light seemed unlikely as species changes ensured a broad range of light optima (Colijn and Van Buurt 1975, Moss 1977), and any dependence upon nutrient status was likewise circumspect (Stanley and Daley 1976). Still, significant, positive correlations existed for the Hastings epipelic photosynthetic index against light, orthophosphate, and silica ($r = 0.420$, $p < 0.25$; $r = 0.540$, $p < 0.10$; $r = 0.640$, $p < 0.10$, respectively).

Hastings epipelic photosynthetic efficiency values showed a range similar to those of other epipelic studies (Hargrave 1969, Kairesalo 1977). Also, the vertical distribution of Hastings photosynthetic efficiencies, increasing with depth, was a pattern

shown previously by Hargrave (1969). But Kairesalo (1977) suggested a decrease with depth and a seasonal increase spring through autumn. In Hastings, the photosynthetic efficiency decreased spring through autumn; that is, it showed a positive response to temperature (1975, $r = 0.440$, $p < 0.25$; 1976, $r = 0.550$, $p < 0.10$), a negative response to bicarbonate (1975, $r = -0.510$, $p < 0.10$; 1976, $r = -0.590$, $p < 0.10$), and a positive response to chlorophyll _a_ standing crop (1975, $r = 0.870$, $p < 0.01$; 1976, $r = 0.490$, $p < 0.25$).

The same increase with depth and decrease spring through autumn occurred for Hastings productivity efficiency. The more complex relationship expressed by the productivity efficiency was not generally correlated with the physico-chemical parameters monitored. The only exception was a good positive correlation against temperature during 1976 ($r = 0.640$, $p < 0.10$).

In general, the three productivity relationships indicated that populations at 0.25 m were most active but those from deeper water were actually more efficient. Hargrave (1969) attributed increased efficiency with depth to increased physical stability and nutrient stability which the Hastings data supports. Moreover, Moss (1977) has shown that epipelic algae are inherently efficient at low light levels, and considers this a definitive characteristic for the epipelic community.

5. EPIPHYTON

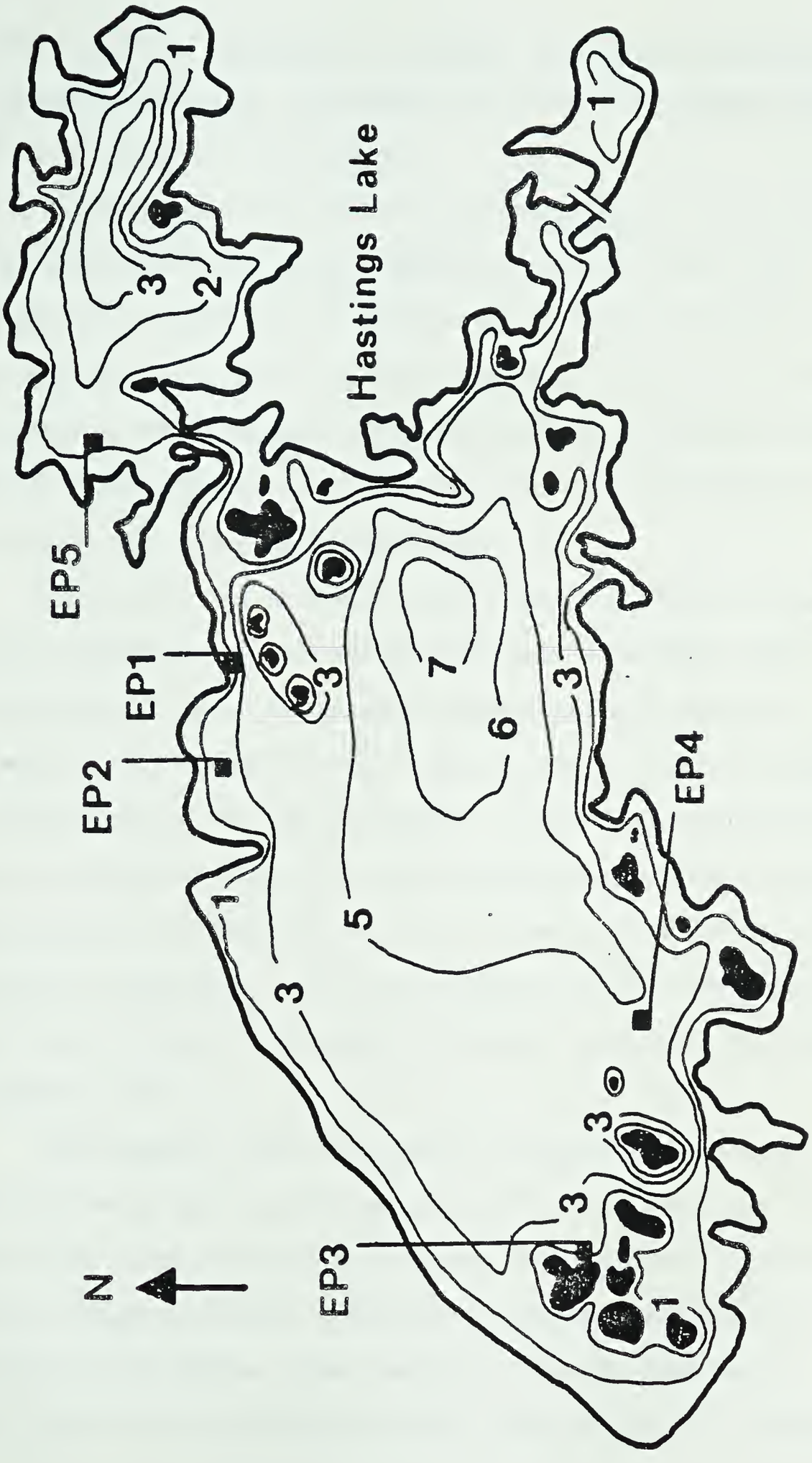
The epiphytic algal community is an integral part of lake ecosystems (Godward 1937, Round 1965, Straskraba and Pieczynska 1970, Wetzel 1975). It is important as a mediator of lake nutrient status, and as a contributor to total lake standing crop and productivity (Wetzel 1964, Wetzel and Allen 1970, Hickman 1971b, Wetzel, et al. 1972).

Reluctance to study the epiphyton can be attributed, in part, to the inherent spatial heterogeneity of the community and the consequent problems of sampling. Efforts directed at facilitating study using artificial substrata have been popular (Cooke 1956, Hohn 1966, Brown and Austin 1971, Eloranta and Kunnas 1976). However, the question of both qualitative and quantitative differences between artificial and natural substrata is posed (Castenholz 1961, Tippett 1970, Evans and Stockner 1972, Brown 1976). Therefore, a study of the epiphyton living attached to natural substrata was designed to ascertain both spatial and temporal distributions of physico-chemical parameters, species, standing crop, and primary productivity in a shallow, eutrophic prairie-parkland lake, and thus provide a community overview of the epiphyton.

5.1. Methods

To ensure reasonable habitat diversity the lake was surveyed before sampling sites were established (Figure 34). Hydrophytes present in the lake included Scirpus validus, Phragmites australis,

Figure 34.
Bathymetric map of Hastings Lake
showing sampling sites for the epiphyton
EP1, EP2, EP3, EP4, and EP5.


Hastings Lake
EP1
EP2
EP3
EP4
EP5
N
1 km
1
2
3
5
6
7

Typha latifolia, Ceratophyllum demersum, Myriophyllum exalbescens, Potamogeton vaginatus, Potamogeton richardsonii, Polygonum amphibia, Lemna trisulca, and Lemna minor.

The epiphyton was collected from the Scirpus at sites EP2, EP3, EP4, and EP5 and from the Phragmites at sites EP1, EP3, EP4, and EP5 (Figure 34). Sites EP1 and EP3 were designated as sheltered sites; EP2 and EP4 as open sites subject to most wave action; and EP5, situated in the northeast portion of the lake, as open but sheltered at the same time since this portion of the lake was much more sheltered than sites in the main basin.

During 1974 the epiphyton growing attached to the current year's growing stems, and the previous year's decaying stems, was sampled at all sites for seasonal distributions of species composition and standing crop. Samples were collected at weekly intervals during the ice free season. During 1975 biweekly samples were collected at sites EP3, EP4, and EP5 for the study of vertical and seasonal distributions of species composition standing crop and primary productivity. For cross incubation studies Phragmites from EP5 were collected in October 1975 and then monthly in the ice free seasons of 1976.

The epiphytic algae were sampled as described by Hickman (1971b) and Hickman and Klarer (1973) with stems being cut 5 cm below the water surface before a glass tube (internal diameter 2.5 cm and length 25 cm) was slipped carefully over the submersed portion and epiphyton. The stem was cut and the tube sealed. Stems for the vertical distribution studies were sampled in a similar

manner, but tree-pruning shears were used to cut the stems which were sealed in 100 cm long glass tubes. These stems were later cut into 25 cm lengths, and subsequently referred to as 25 cm (5-30 cm), 50 cm (30-55 cm) and 75 cm (55-80 cm) sections. The water and loosely attached, or loosely associated, algae,ie. metaphyton (Round 1965), were poured off, and made up to a known volume for species composition and standing crop determinations. The attached algae were then removed into a known volume by carefully scraping the stem with a scalpel (Hickman 1971b, Hickman and Klarer 1973). Finally the scraped area was determined.

5.1.1. Physico-chemical Parameters

Incident irradiance during the incubation period was determined using an actinograph (C.F. Cassella, London) calibrated against a Kipp solarimeter. Underwater light penetration was determined using a quantum sensor measuring quanta in photosynthetically available radiation (400-700 nm) (LI-185, Lambda Instruments). Further light data was obtained from Environment Canada meteorological records.

Water temperatures and dissolved oxygen were measured using a Yellow Springs Instrument model 54 oxygen-temperature meter.

Water samples were collected from each site for chemical analysis, after filtration through Whatman GF/C filters, following procedures outlined in the American Public Health publication (1971). Total alkalinity and pH were determined in the field; the latter being measured with a Radiometer Model 29 pH meter.

The determinations for potassium, sodium, calcium, carbonate,

copper, magnesium, manganese, and zinc done for the phytoplankton were not done for the epiphyton. All other chemistry followed methods outlined for the phytoplankton (3.1.1. Physico-chemical Parameters).

5.1.2. Species

Species identification and enumeration followed procedures stated for the phytoplankton (3.1.2. Species) and epipelon (4.1.2. Species). A subsample was treated with potassium dichromate and concentrated sulfuric acid for subsequent diatom identifications. Another subsample was sedimented for identifications and enumerations using the inverted microscope method (Lund, et al. 1958). Cell count data presented is the mean from all sites. A coefficient of variation calculated for a total count in each of the four seasons and for a representative dominant species in each of the four seasons follows: spring total count 20%, spring dominant Chlamydomonas spp. 24%; summer total count 28%, summer dominant Cocconeis placentula 19%; autumn total count 17%, autumn dominant Lyngbya lagerheimii 25%, winter total count 20%, winter dominant Stigeoclonium nanum 12%.

Mean cell counts were used to calculate the three diversity indices. Richness, evenness, and general diversity were determined as they were for the phytoplankton (3.1.2. Species).

5.1.3. Chlorophyll a

Another subsample was filtered onto Whatman GF/C glass fiber

filters for chlorophyll *a* analysis. The spectrophotometric method and equations of Moss (1967a,b), which correct for the amount of naturally occurring pheophytin *a* were used. All samples were homogenized in 90% acetone to ensure complete extraction, thus repeating procedures from the phytoplankton and epipelon as closely as possible. A coefficient of variation was calculated for a chlorophyll *a* determination in each of the four seasons: spring 20%, summer 17%, autumn 14%, winter 10%.

5.1.4. Productivity

Productivity experiments were virtually restricted to the ice free period. Sub-samples provided duplicate light bottles and one dark bottle for 4 hr (1000-1400 hr) *in situ* incubations. Productivity was determined using the carbon-14 technique modified from Hickman (1971b) and Hickman and Klarer (1973) to include the acid bubbling procedure of Schindler, *et al*. (1972), and subsequent scintillation counting using a Nuclear Chicago Mark I Scintillation Computer, Model 6860. (The carbon-14 was added as $NaHC^{14}O_3$- 5 μCi per 125 ml bottle). A coefficient of variation for productivity values from three seasons follows: spring 9%, summer 9%, autumn 9%.

5.1.5. Cross Incubation Studies

Experiments were designed not only to measure variations in epiphytic algal primary productivity but also to measure the photosynthetic capacity of the populations living at different depths upon the host stems to determine if populations found lower

down the host stem possessed the same, greater, or lesser, photosynthetic capacity as those nearer the water surface. The experimental design was simple, and involved incubating samples collected from three depths at these, and all other depths (Patten 1963, Elster 1965, Patten and Chabot 1966, Hillbricht-Ilkowska, et al. 1972, Hickman 1973, 1976a).

5.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

The three productivity relationships utilized were calculated as they were for the phytoplankton (3.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency).

5.2. Results

5.2.1. Physico-chemical Parameters

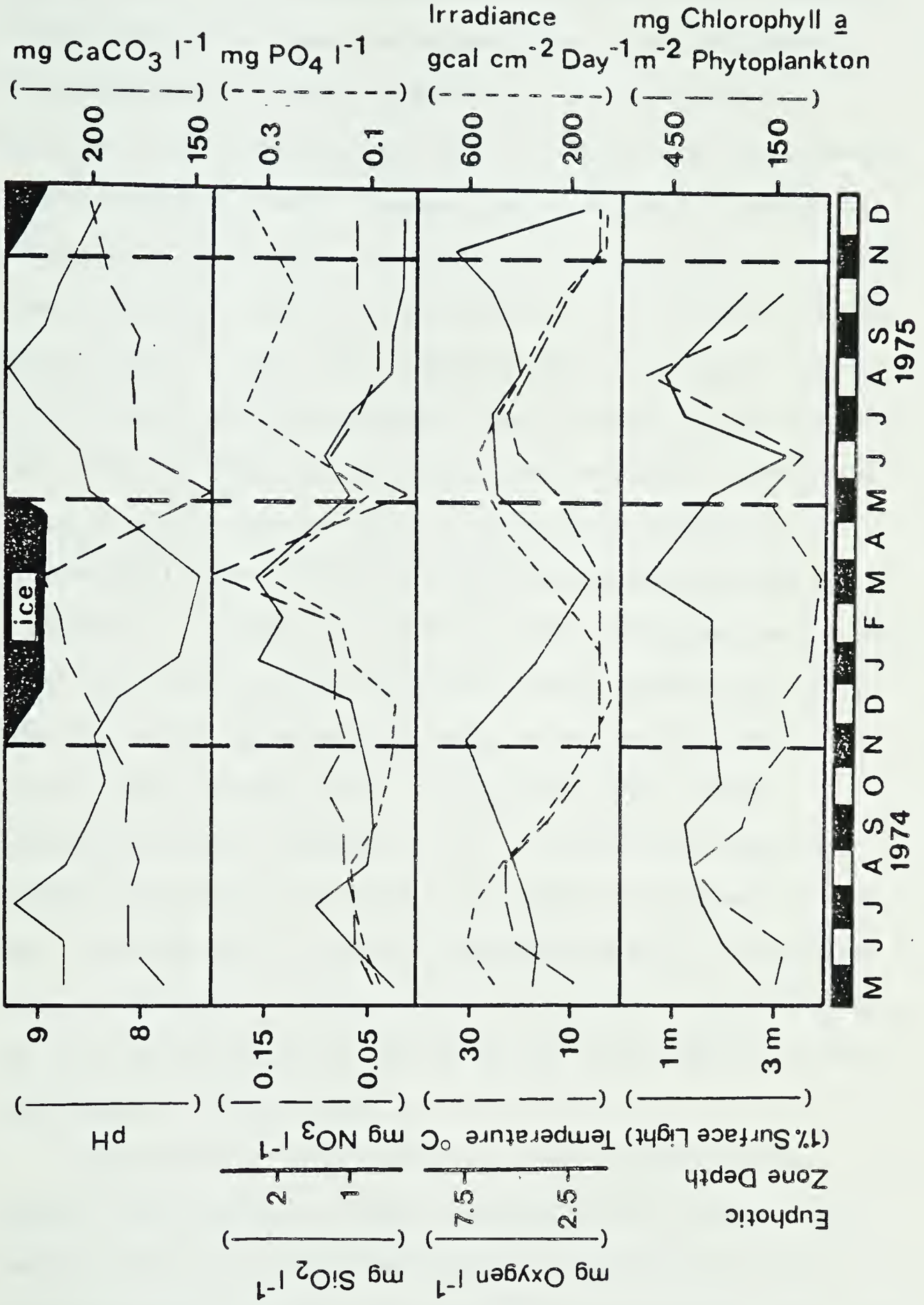
Collated chemistry data from 1974, which represents the period of weekly sampling from the five sites, is presented in Table 7. The respective means and seasonal fluctuations for pH, total alkalinity, and nitrate are similar among all sites. The overall means are representative of lakewide conditions. Mean dissolved silica and orthophosphate follow the same pattern except at site EP5 which has higher mean values.

Data combined from all sites are presented to illustrate seasonal changes during 1974 and 1975 (Figure 35). These approximate lakewide conditions. Each year pH increased from spring to a summer maximum of 9.2, and then decreased to mid-winter minimum

Table 7. The mean and standard deviation of pH, total alkalinity, dissolved silica, nitrate-nitrogen and phosphate-phosphorus at each site for 1974 data from the epiphyton.

Site	pH	Total Alkalinity meq l^{-1}	SiO_2	PO_4-P mg l^{-1}	NO_3-N
EP1	8.63±0.43	3.88±0.22	0.81±0.27	0.12±0.28	0.06±0.02
EP2	8.61±0.39	3.90±0.24	0.66±0.24	0.07±0.09	0.06±0.02
EP3	8.68±0.50	3.90±0.24	0.69±0.21	0.07±0.05	0.07±0.02
EP4	8.67±0.30	3.84±0.36	0.65±0.27	0.05±0.04	0.07±0.04
EP5	8.51±0.62	3.41±0.40	1.83±2.47	1.37±5.67	0.07±0.03
Overall Mean	8.62±0.45	3.79±0.29	0.93±0.69	0.34±1.23	0.07±0.03

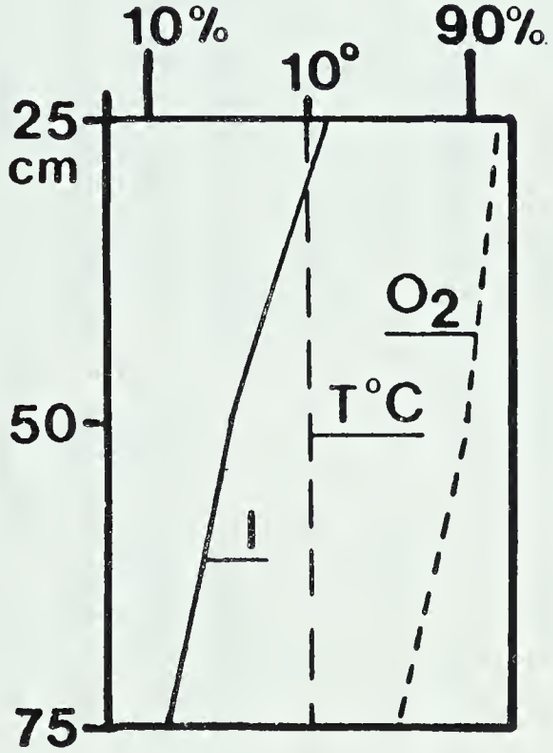
Figure 35.
Seasonal distribution of pH, alkalinity as mg $CaCO_3$/l, mg SiO_2/l, mg NO_3/l, mg PO_4/l, mg O_2/l, temperature °C, surface irradiance in gcal/cm^2/day, euphotic zone depth as 1% surface irradiance; and mg chlorophyll *a*/m^3 phytoplankton for the epiphyton.


mg CaCO3 l-1
mg PO4 l-1
Irradiance
gcal cm-2 Day-1
mg Chlorophyll a
m-2 Phytoplankton
200
150
0.3
0.1
600
200
450
150
ice
M J J A S O N D J F M A M J J A S O N D
1974
1975
9
8
0.15
0.05
30
10
1 m
3 m
pH
mg NO3 l-1
Temperature °C
(1% Surface Light)
Euphotic
Zone Depth
2
1
7.5
2.5
mg SiO2 l-1
mg Oxygen l-1

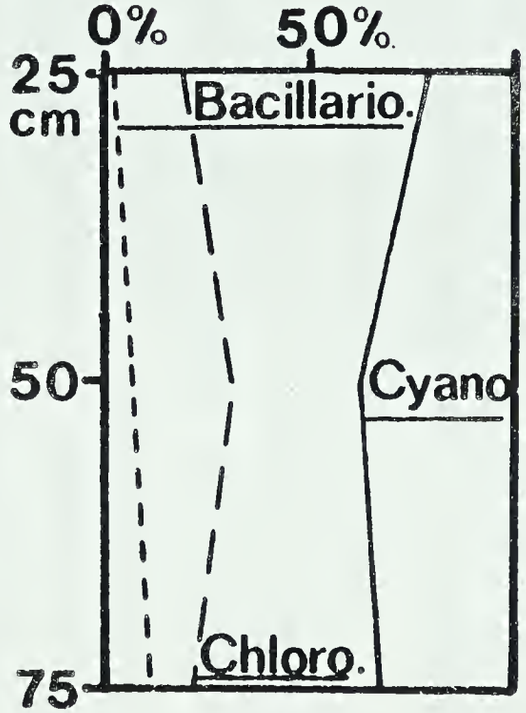
values of 7.4. Total alkalinity was lowest each spring, increased slightly during the summer and autumn before increasing rapidly during the winter to reach maximum values in late February. Dissolved silica concentrations were also highest during the winter months reaching 2.4 mg/l. However, they were low each spring and autumn at 0.2 to 0.5 mg/l. Nitrate concentrations slowly increased from a minimum in May 1974 to an autumn peak. This trend continued under winter ice cover until a large maximum of 0.21 mg/l occurred in March 1975. As the ice melted values decreased rapidly such that each spring minimum nitrate concentrations occurred. A small peak occurred in early summer in 1975. The seasonal patterns of orthophosphate were similar each year with summer and winter peaks. A maximum of 0.30 mg/l was recorded in March 1975 under ice and snow cover, and values in 1975 were generally much higher than in 1974. Dissolved oxygen concentrations peaked in spring and autumn, and lowest values occurred under the ice during winter. Water temperature reached a maximum of 22 °C in July of both years and incident irradiance levels were also highest in the summer of each year, one month earlier than the temperature maxima. The euphotic zone, as defined by the depth of the 1% light level ranged from 0.5 to 3.2 m; decreasing during the summer due to development of large phytoplankton standing crops.

During vertical distribution and cross incubation studies vertical distributions of oxygen, temperature and irradiance were measured (Figure 36). The mean dissolved oxygen concentration for the 25 cm interval was 98% saturation (following Mortimer 1956); for

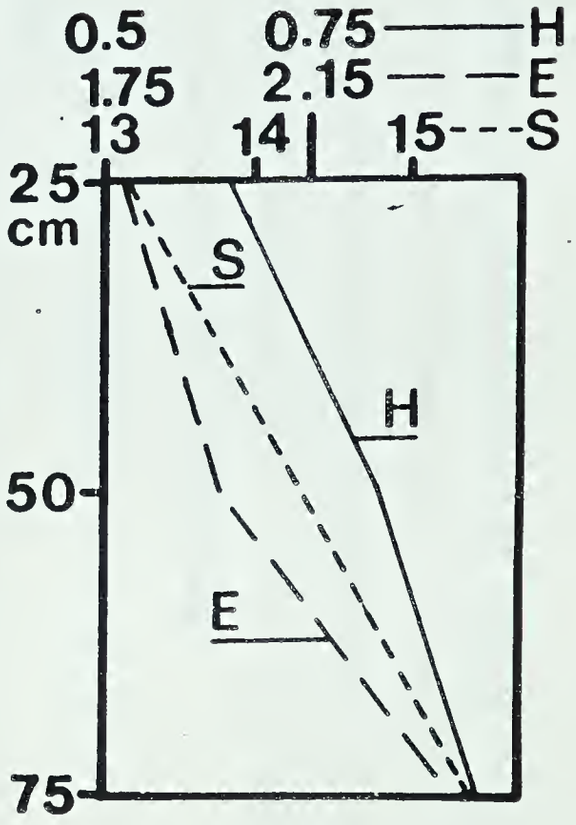
Figure 36.
Vertical distribution of % irradiance (I) based on 100% surface irradiance in pelagial zone, of % oxygen saturation (O), and of temperature (C) in graph A; vertical distribution of % algal divisions in graph B; and vertical distribution of species richness (---S---), of species evenness (_ _E _ _), and of Shannon's diversity (_ _H _ _) for the epiphyton.


10%
10°
90%
25
cm
50
75
O2
T°C
I

A


0%
50%
25
cm
50
75
Bacillario.
Cyano
Chloro.

B


0.5
0.75
H
1.75
2.15
E
13
14
15
S
25
cm
50
75
S
H
E

C

the 50 cm interval 90%, and for the 75 cm interval 75%. Temperatures were always isothermal while the mean irradiance just below the water surface within the macrophyte beds was 55% of that determined similarly outside the bed. At the 50 cm and 75 cm levels irradiance averaged 30% and 15%, respectively.

5.2.2. Species

Sixteen of the 120 taxa identified from the epiphyton were considered dominants, ie. made up at least 20% of the cell counts at any one time (Table 8). Seven of those dominants were considered planktonic, but were found as components of the epiphyton. The remaining nine dominants were considered benthic.

None of the species considered planktonic showed any consistent vertical distribution in the epiphyton, and so seasonal graphs have been made of mean data (Figure 37). Oscillatoria subbrevis and Cyclotella meneghiniana had spring and autumn peaks; Anabaena flos-aquae had summer peaks, while Microcystis aeruginosa displayed both summer and autumn peaks. Merismopedia tenuissima and Chlamydomonas spp. were largest in spring, summer, and autumn. Coelosphaerium naegelianum showed peaks in all four seasons.

Seven of the nine benthic dominants showed recognizable depth distribution. Those prefering the top 25 cm of the host stems included Lyngbya diguetii, Calothrix sp., Rivularia haematites, and Stigeoclonium nanum (Figure 38). Lyngbya diguetii peaked late in the spring, then decreased sharply, and increased again to produce autumn maxima (Figure 37). Its cell counts remained relatively high

Table 8. Dominant species found in the epiphyton.

CYANOPHYTA

Anabaena flos-aquae (Lyngb.) Breb.
Calothrix sp.
Coelosphaerium naegelianum Unger
Lyngbya diguetii Gomont
Merismopedia tenuissima Lemm.
Microcystis aeruginosa (Kutz.) Elenkin
Oscillatoria subbrevis Schmidle
Rivularia haematites (D.C.) C.A. Agardh

CHLOROPHYTA

Chlamydomonas spp.
Stigeoclonium nanum Kutz.

BACILLARIOPHYTA

Cocconeis placentula Ehr.
Cyclotella meneghiniana Kutz.
Gomphonema parvulum Kutz.
Nitzschia spp.
Rhoicosphenia curvata (Kutz.) Grun.
Synedra acus Kutz.

Figure 37.
Seasonal distribution of
Lyngbya diguetii, *Oscillatoria subbrevis*,
Rivularia haematites, *Calothrix*
species, *Merismopedia tenuissima*,
Anabaena flos-aquae, *Microcystis aeruginosa*,
Coelosphaerium naegelianum, *Stigeoclonium*
nanum, *Chlamydomonas* species,
Cocconeis placentula, *Nitzschia* species,
Rhoicosphenia curvata, *Cyclotella meneghiniana*,
Gomphonema parvulum,
and
Synedra acus
per m^2 host stem for the epiphyton.

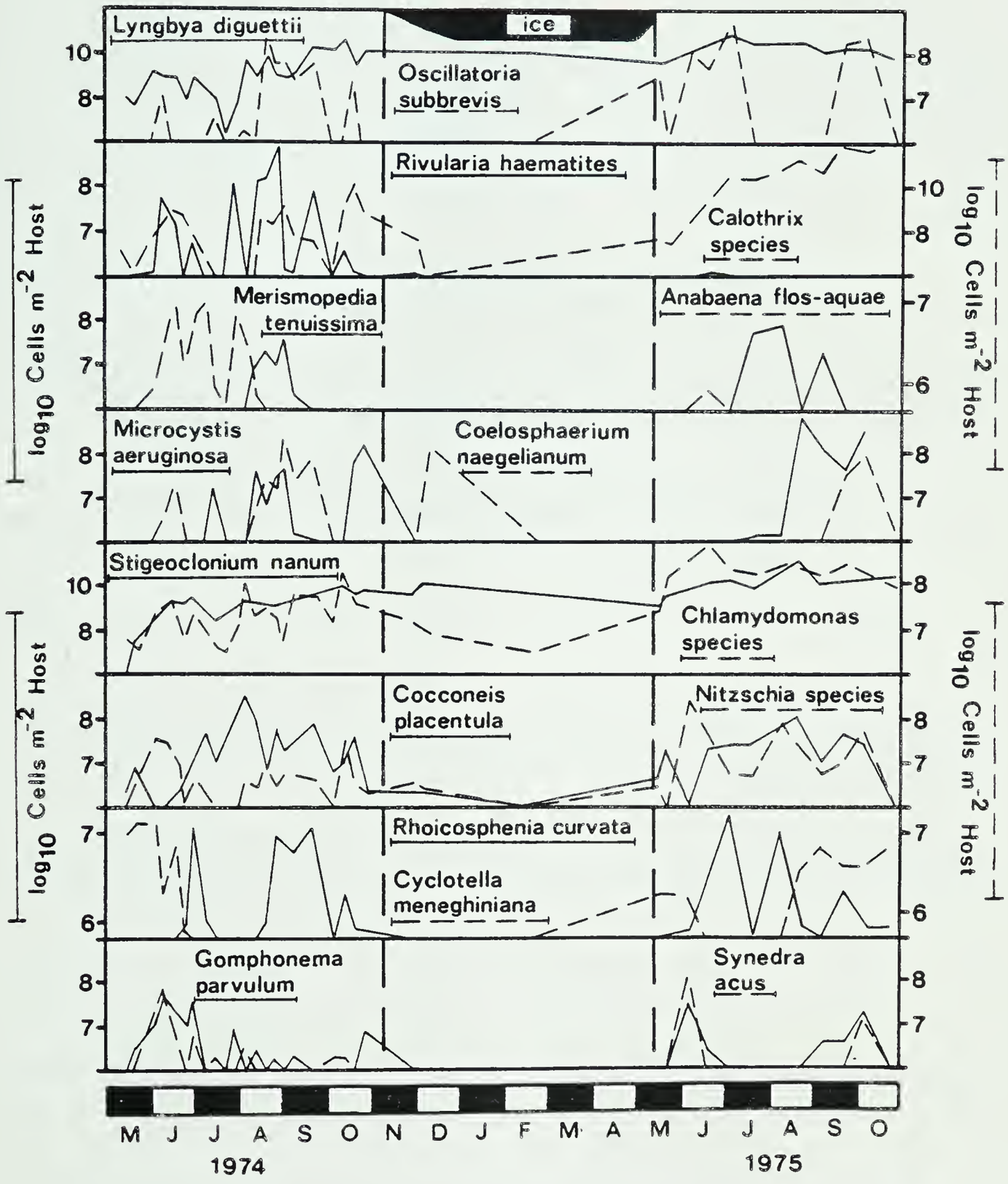
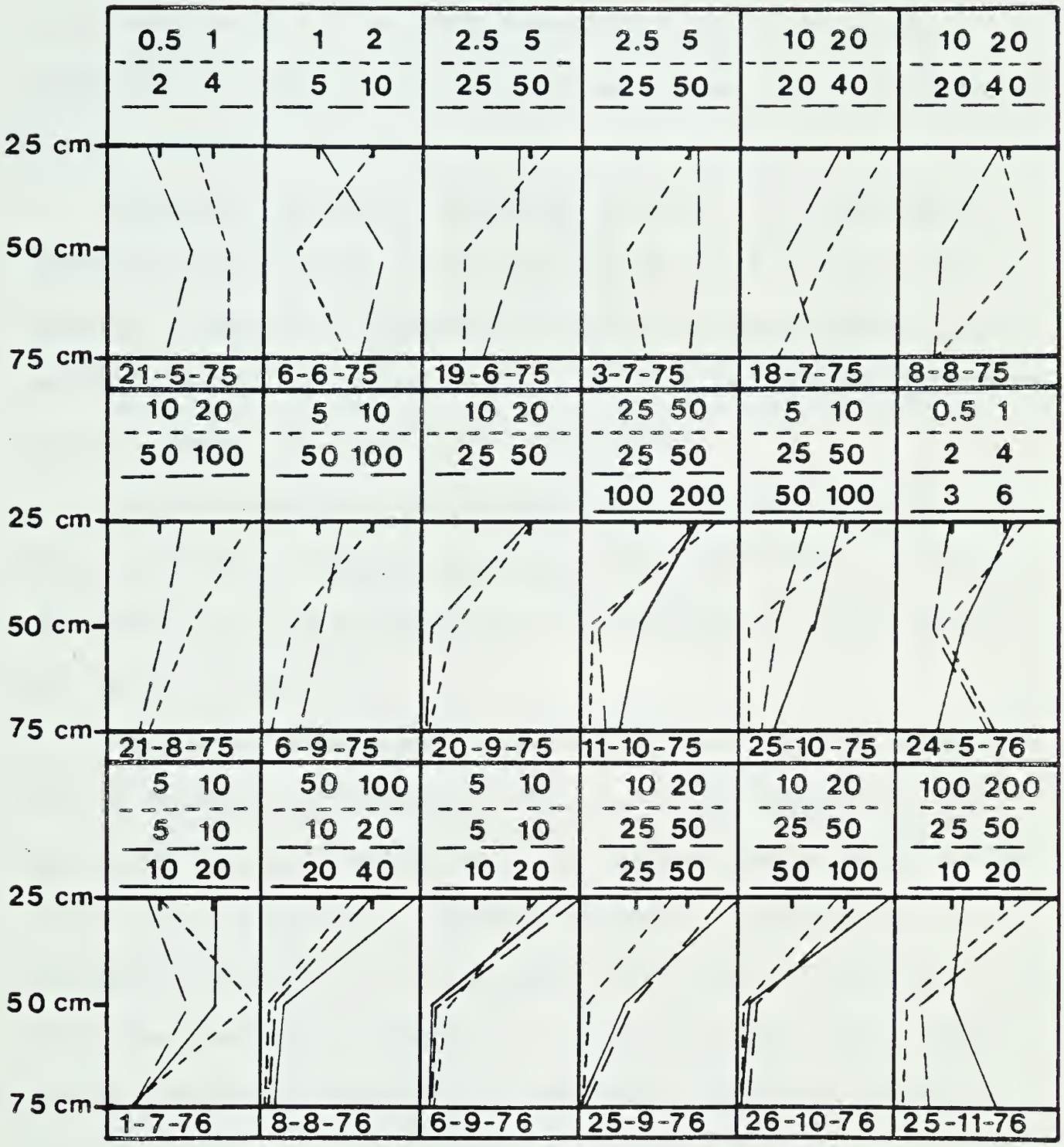

Lyngbya diguettii
ice
Oscillatoria subbrevis
Rivularia haematites
Calothrix species
Merismopedia tenuissima
Anabaena flos-aquae
Microcystis aeruginosa
Coelosphaerium naegelianum
Stigeoclonium nanum
Chlamydomonas species
Cocconeis placentula
Nitzschia species
Rhoicosphenia curvata
Cyclotella meneghiniana
Gomphonema parvulum
Synedra acus
log10 Cells m-2 Host
M J J A S O N D J F M A M J J A S O
1974
1975

Figure 38.
Vertical distributions of
Stigeoclonium nanum
(_____),
Lyngbya diguetii
(-----), and
Calothrix
species (.....) per m^2 host stem
for the epiphyton.


0.5 1
2 4
1 2
5 10
2.5 5
25 50
2.5 5
25 50
10 20
20 40
10 20
20 40
25 cm
50 cm
75 cm
21-5-75
6-6-75
19-6-75
3-7-75
18-7-75
8-8-75
10 20
50 100
5 10
50 100
10 20
25 50
25 50
25 50
100 200
5 10
25 50
50 100
0.5 1
2 4
3 6
25 cm
50 cm
75 cm
21-8-75
6-9-75
20-9-75
11-10-75
25-10-75
24-5-76
5 10
5 10
10 20
50 100
10 20
20 40
5 10
10 20
10 20
25 50
25 50
50 100
100 200
25 50
10 20
25 cm
50 cm
75 cm
1-7-76
8-8-76
6-9-76
25-9-76
26-10-76
25-11-76

during winter. The Calothrix species, Rivularia haematites, and Stigeoclonium nanum showed spring, summer, and autumn increases (Figure 37). For Stigeoclonium nanum cell counts were relatively high in winter also. Of the aforementioned benthic dominants, Stigeoclonium nanum was the only species to show consistent peaks through more than one year.

Cocconeis placentula, Gomphonema parvulum, and Rhoicosphenia curvata developed their largest populations in 50 and 75 cm depth regions (Figure 39). Gomphonema parvulum and Rhoicosphenia curvata exhibited spring and autumn peaks, while Cocconeis placentula showed spring, summer, and autumn peaks (Figure 37).

The two remaining benthic species did not appear to show any depth preference. Synedra acus populations were largest in spring and autumn, and the Nitzschia spp. were largest in spring, summer, and autumn (Figure 37).

In general, cyanophycean algae were found in largest numbers in the 25 cm region; chlorophycean algae in largest numbers in the 50 cm region; and bacillariophycean algal numbers were greatest in the 75 cm region (Figure 36). Based on 25 cm cell counts, the Cyanophyta accounted for the greatest cell numbers (Figure 40). The blue-greens were most important in the summer (Figure 40). Members of the Chlorophyta were almost as important, and were of special note in winter. The Bacillariophyta comprised more than 1% of the total counts only on occasion, most notably in spring and autumn. Each of these algal groups increased in numbers spring through autumn and then decreased in winter.

Figure 39.
Vertical distributions of
Cocconeis placentula
(____),
Rhoicosphenia curvata
(-----),
and
Gomphonema parvulum
(.....) per m^2 host stem
for the epiphyton.

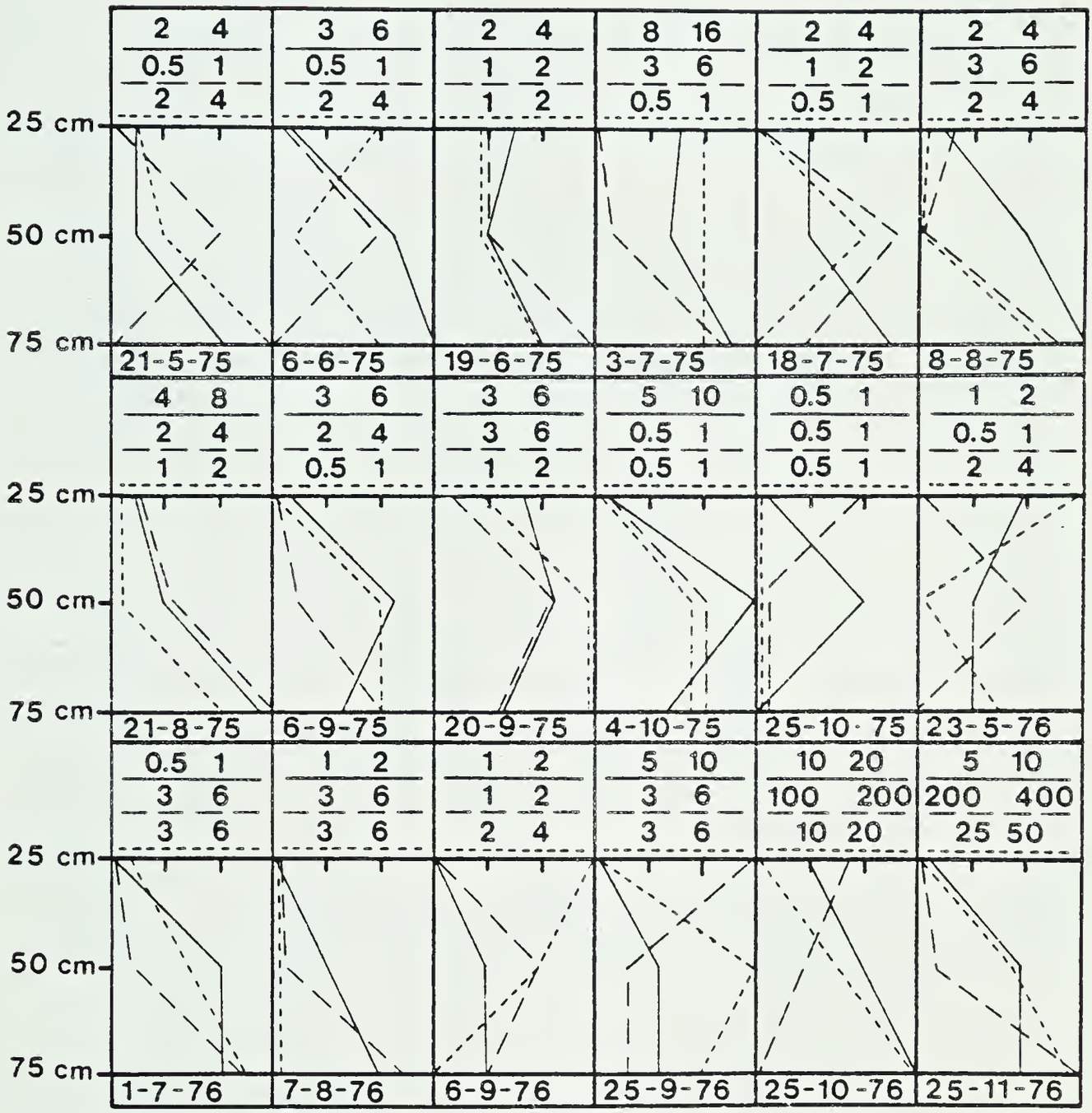
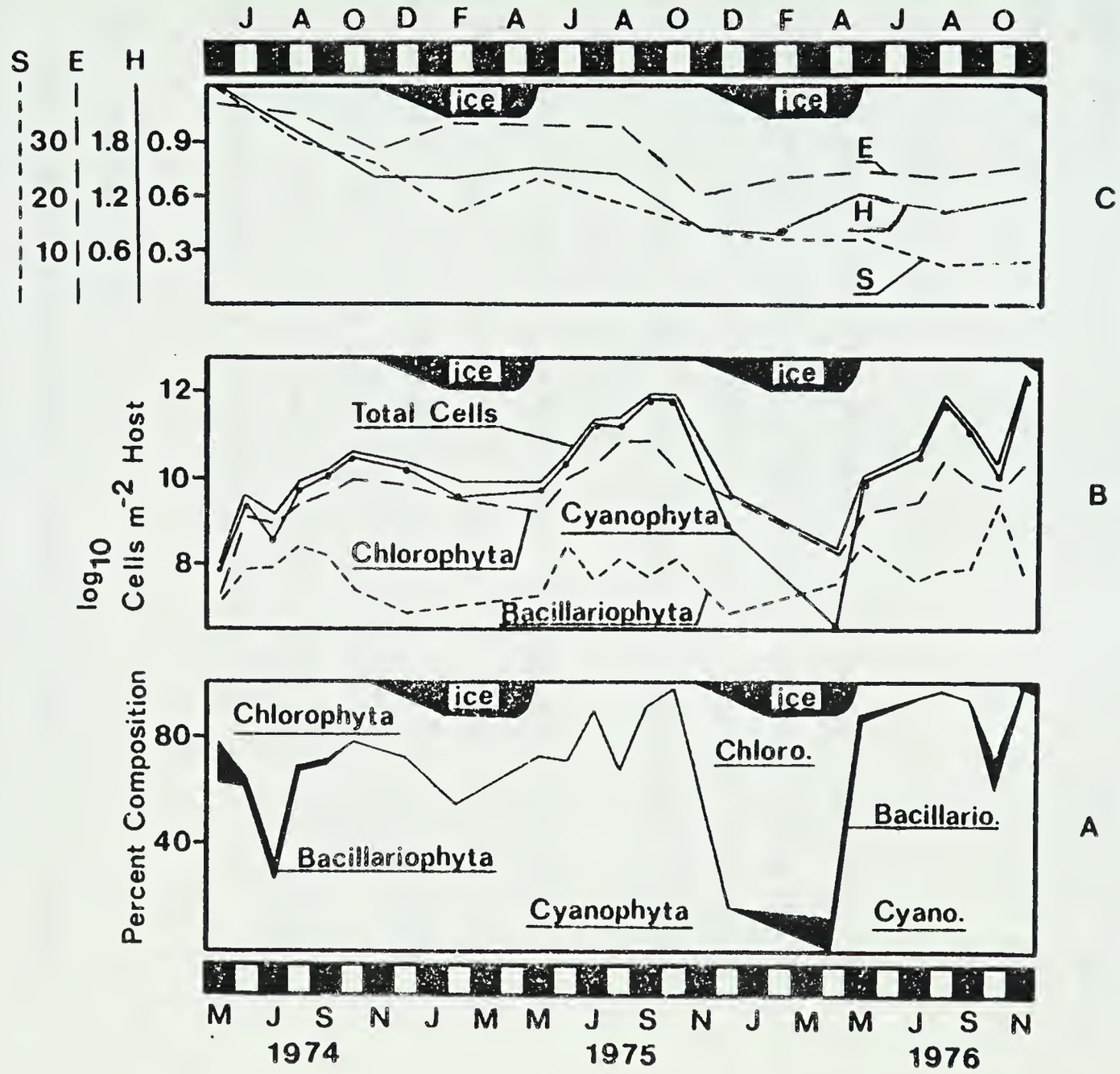

25 cm
50 cm
75 cm
2 4 / 0.5 1 / 2 4
21-5-75
3 6 / 0.5 1 / 2 4
6-6-75
2 4 / 1 2 / 1 2
19-6-75
8 16 / 3 6 / 0.5 1
3-7-75
2 4 / 1 2 / 0.5 1
18-7-75
2 4 / 3 6 / 2 4
8-8-75
4 8 / 2 4 / 1 2
21-8-75
3 6 / 2 4 / 0.5 1
6-9-75
3 6 / 3 6 / 1 2
20-9-75
5 10 / 0.5 1 / 0.5 1
4-10-75
0.5 1 / 0.5 1 / 0.5 1
25-10-75
1 2 / 0.5 1 / 2 4
23-5-76
0.5 1 / 3 6 / 3 6
1-7-76
1 2 / 3 6 / 3 6
7-8-76
1 2 / 1 2 / 2 4
6-9-76
5 10 / 3 6 / 3 6
25-9-76
10 20 / 100 200 / 10 20
25-10-76
5 10 / 200 400 / 25 50
25-11-76

Figure 40.
Seasonal distribution of percent composition
for algal divisions in graph A,
of cell counts for algal divisions and total
cells in graph B, and of species richness
(---S---), species evenness (_ _ _ E _ _ _),
Shannon's diversity (_ H _) in graph C for the epiphyton.


J A O D F A J A O D F A J A O
S E H
30 1.8 0.9
20 1.2 0.6
10 0.6 0.3
ice
ice
E
H
S
C
log10 Cells m-2 Host
12
10
8
Total Cells
Cyanophyta
Chlorophyta
Bacillariophyta
B
Percent Composition
80
40
Chlorophyta
Bacillariophyta
Cyanophyta
Chloro.
Bacillario.
Cyano.
A
M J S N J M M J S N J M M J S N
1974
1975
1976

The three species diversity indices used to represent overall community species fluctuations have been presented as depth distributions (Figure 36). Species richness, evenness, and general diversity each increased with depth. All three indices were generally highest in spring and decreased summer, autumn, and winter (Figure 40).

5.2.3. Standing Crop

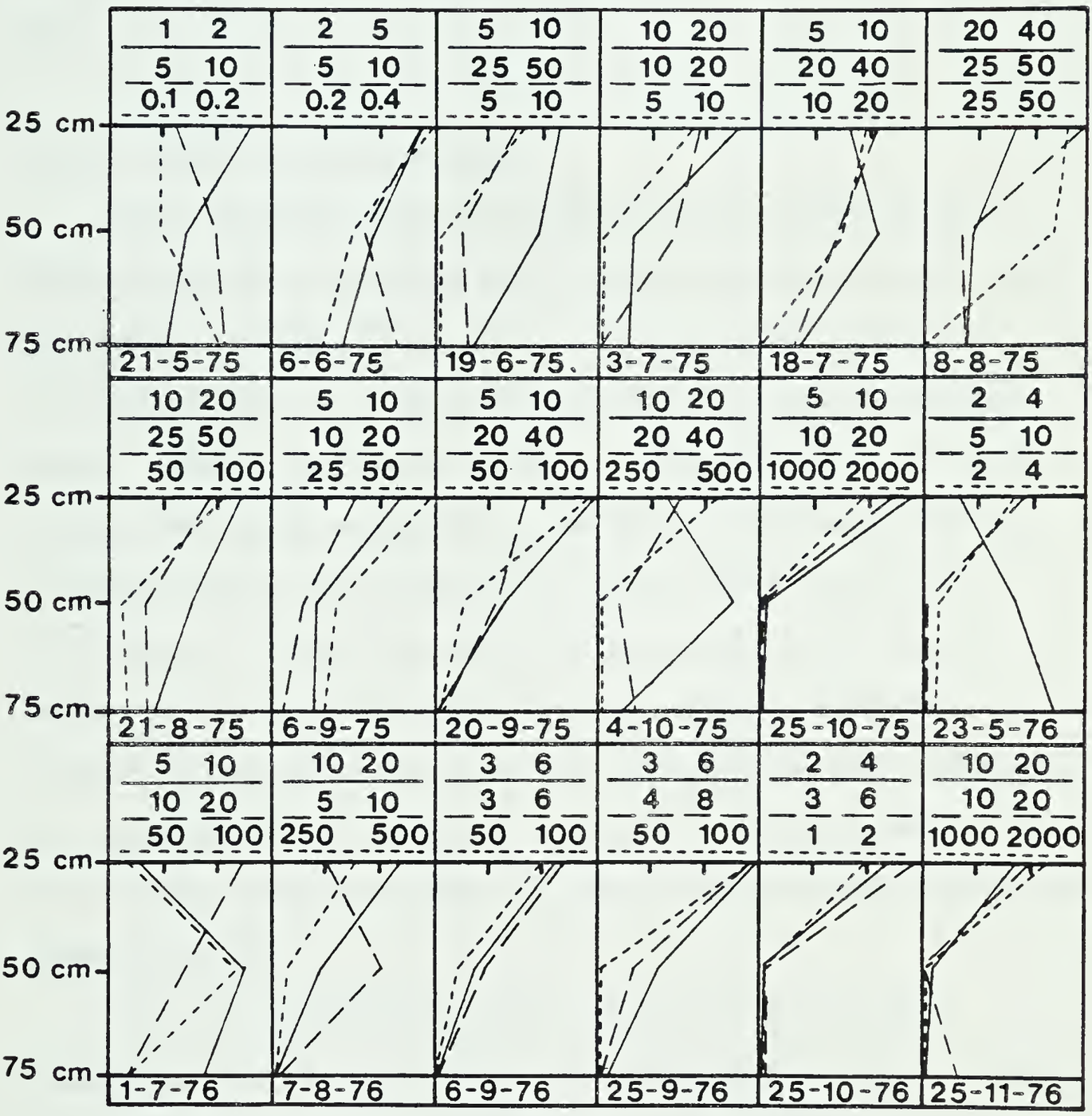
Both mean total cell count and chlorophyll a data showed the highest standing crops were almost always in the 25 cm region and the least in the 75 cm interval (Figure 41). In the first half of the ice free season there was a tendency for the maximum standing crop to be in the 50 cm region.

Seasonal trends in standing crop for the 25 cm interval displayed a peak in spring 1974, then a mid-summer minimum, and then an increase to a large autumn maximum (Figure 42). The standing crop decreased in size under winter ice-cover, but did not disappear. These trends were repeated in 1975, and to a lesser extent with respect to the spring peak in 1976.

5.2.4. Productivity

The vertical distribution of epiphytic productivity followed standing crop closely, decreasing with depth and decreasing irradiance levels (Figure 41). However, incubations performed under 10 cm of ice and 1 cm of fresh snow in November 1976, showed the highest productivity at the 75 cm interval even though the standing

Figure 41.
Vertical distribution of cell counts per m^2 host stem (-----), mg chlorophyll a per m^2 host stem (_____), and mg carbon per m^2 host stem per hour (_____) for the epiphyton.


25 cm
50 cm
75 cm
1 2 / 5 10 / 0.1 0.2
21-5-75
2 5 / 5 10 / 0.2 0.4
6-6-75
5 10 / 25 50 / 5 10
19-6-75
10 20 / 10 20 / 5 10
3-7-75
5 10 / 20 40 / 10 20
18-7-75
20 40 / 25 50 / 25 50
8-8-75
10 20 / 25 50 / 50 100
21-8-75
5 10 / 10 20 / 25 50
6-9-75
5 10 / 20 40 / 50 100
20-9-75
10 20 / 20 40 / 250 500
4-10-75
5 10 / 10 20 / 1000 2000
25-10-75
2 4 / 5 10 / 2 4
23-5-76
5 10 / 10 20 / 50 100
1-7-76
10 20 / 5 10 / 250 500
7-8-76
3 6 / 3 6 / 50 100
6-9-76
3 6 / 4 8 / 50 100
25-9-76
2 4 / 3 6 / 1 2
25-10-76
10 20 / 10 20 / 1000 2000
25-11-76

crop was largest in the 25 cm region.

On a seasonal basis the 25 cm interval showed a spring peak in productivity, a summer decline, and an autumn maximum during 1975. In 1976 only an autumn maximum was shown for productivity (Figure 42).

5.2.5. Cross Incubation Studies

Cross incubation studies indicated that for each collection depth productivity decreased with increased incubation depth, hence decreased irradiance (Figure 43). The algae collected at 25 cm generally yielded the highest mean productivity at each suspension depth. However, variations did occur. The two October 1975 dates showed the highest productivity from the 25 cm collection at each suspension depth, but in May 1976, results were mixed, while in July, algae collected from the 50 cm interval gave the highest values at each suspension depth. Again in August, September, and October at each suspension depth the highest values were attained by the algae collected from the 25 cm interval. But in November under ice and snow cover it was the collection from 75 cm that yielded the highest results.

The mean photosynthetic index decreased with increased suspension depth for each of the collection depths (Table 9, Figure 44). Those collections from 75 cm tended to produce the highest values at each suspension depth. The two October 1975 studies showed algae from 50 cm collections were most active, and in May 1976, it was those from 25 cm. But from July to October 1976, the

Figure 42.
Seasonal distribution of cell counts per m^2 host stem (_____), mg chlorophyll *a* per m^2 hosts stem (---), and mg carbon per m^2 host stem per hour (.....) for the epiphyton.

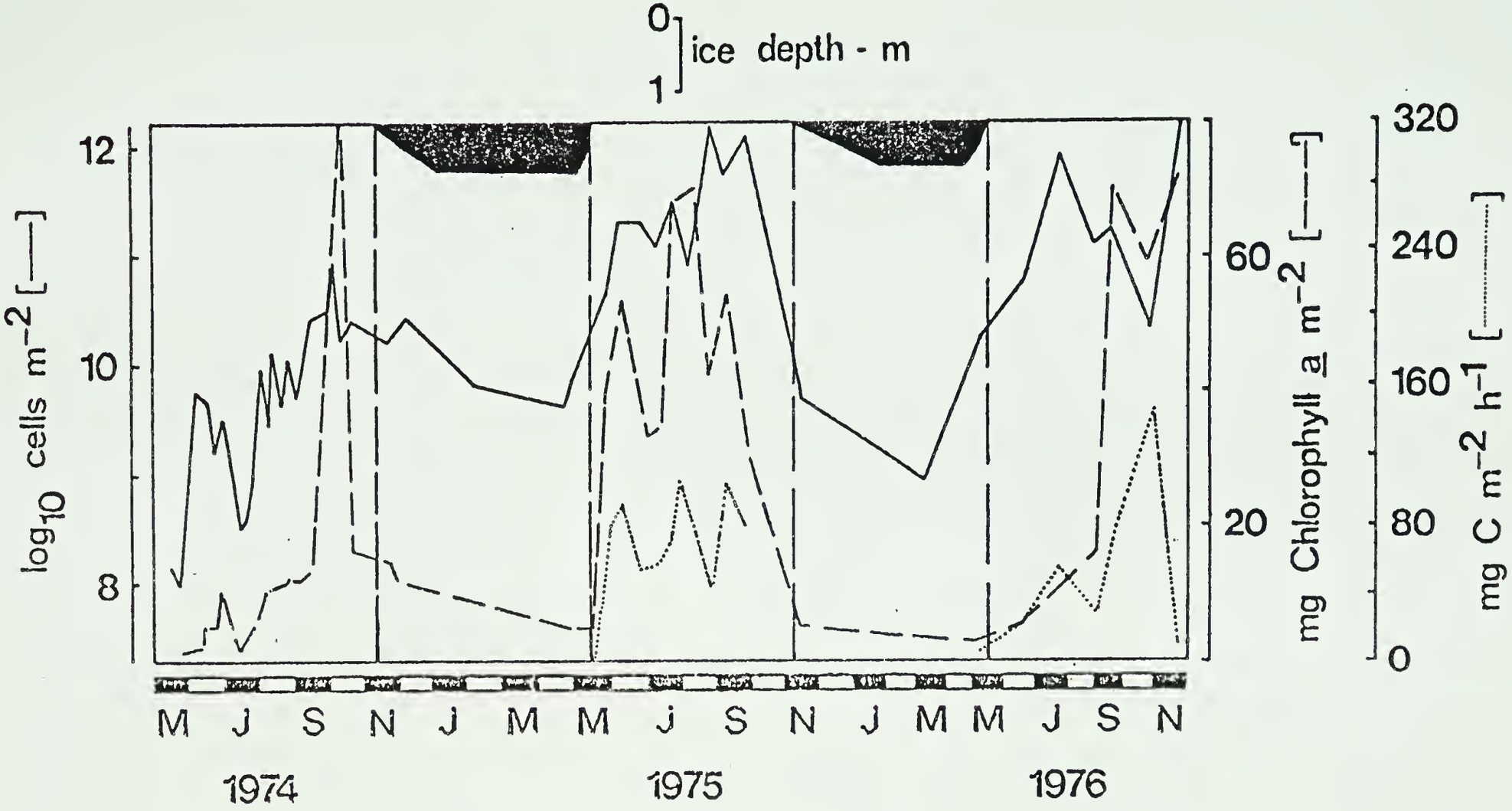

0
1
ice depth - m
12
10
8
log10 cells m-2 [——]
60
20
mg Chlorophyll a m-2 [– – –]
320
240
160
80
0
mg C m-2 h-1 [·····]
M J S N J M M J S N J M M J S N
1974
1975
1976

Figure 43.
Epiphyton productivity expressed
as a function of collection
and incubation depth.

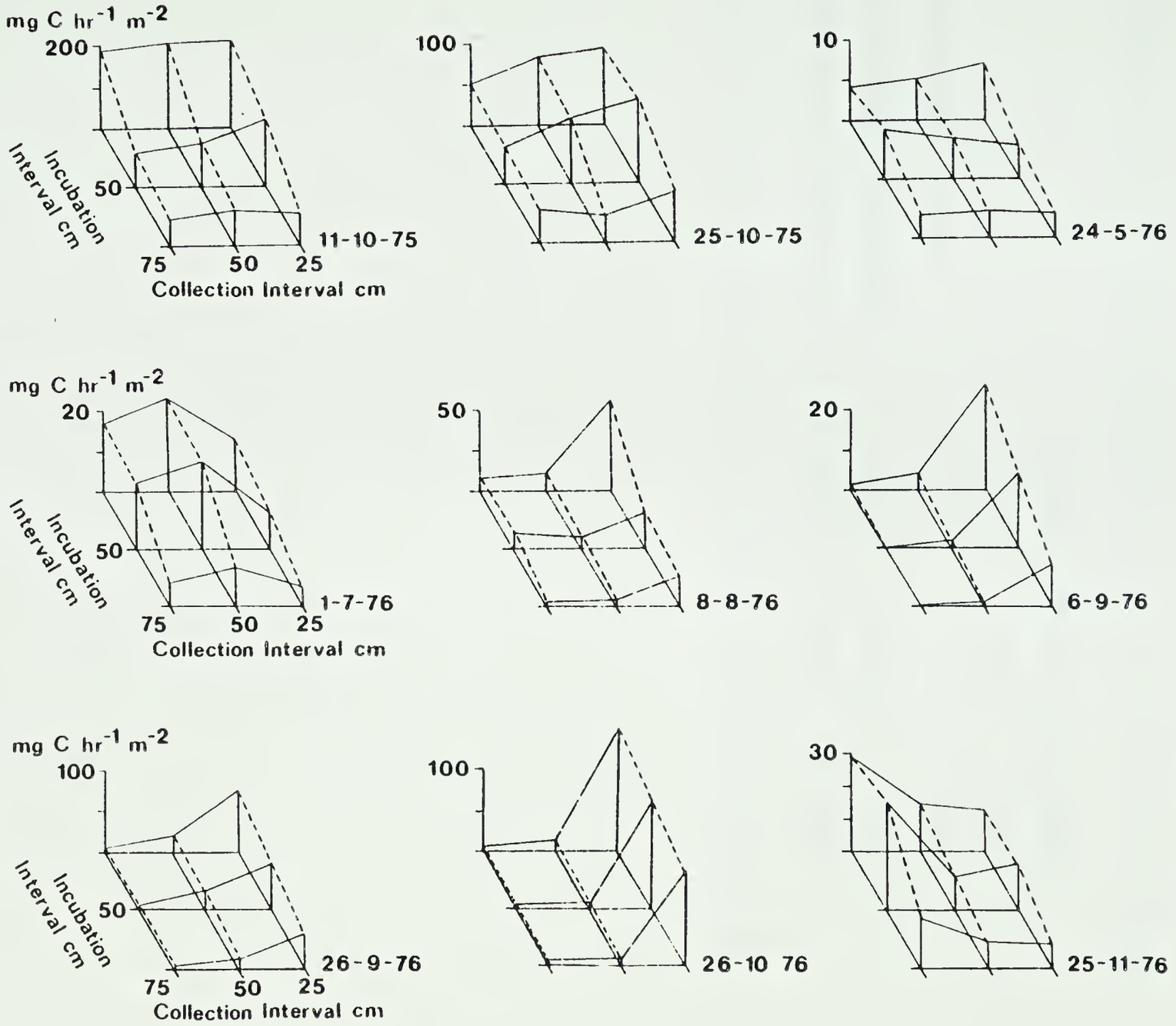
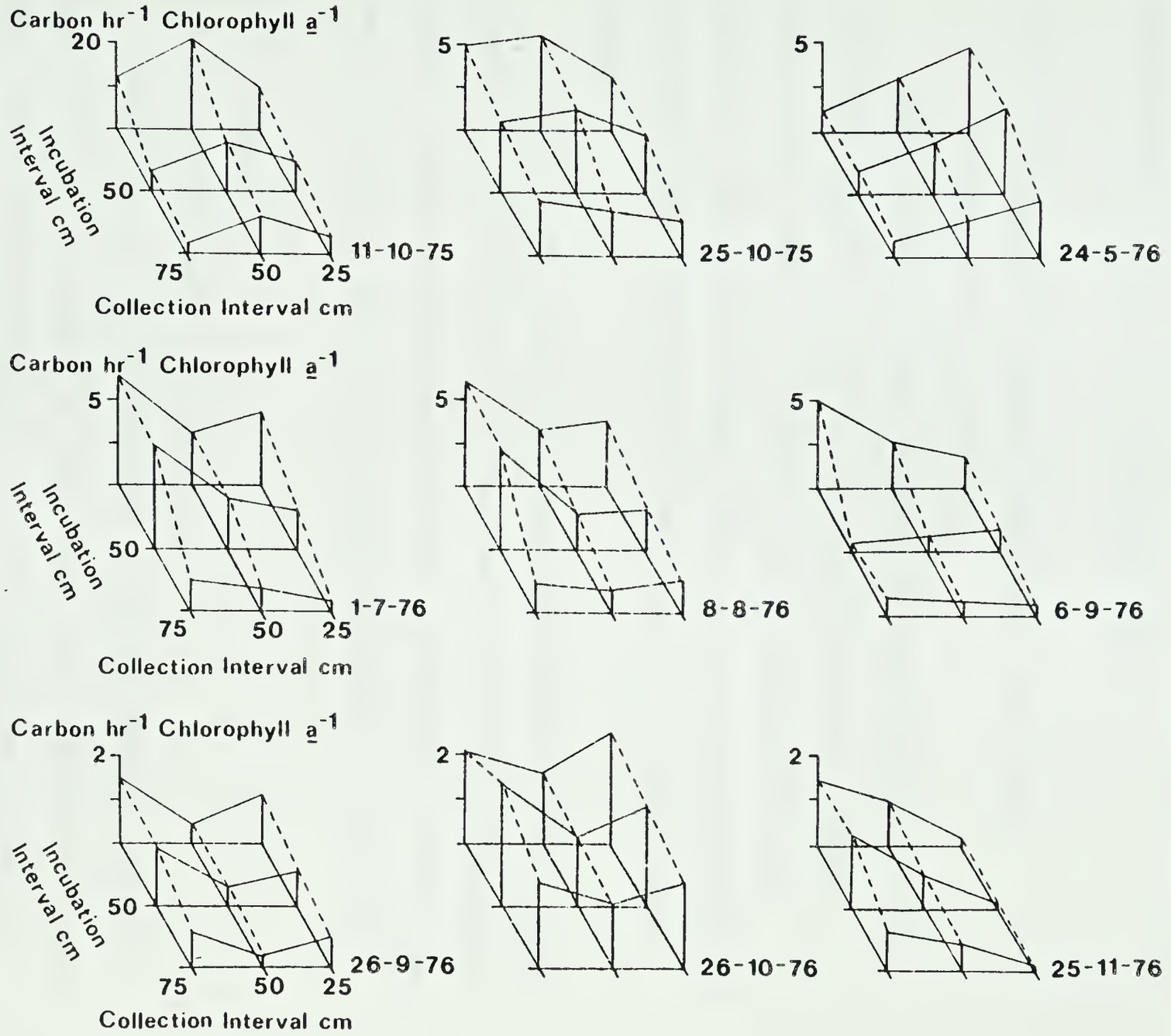

mg C hr-1 m-2
200
50
Incubation Interval cm
75
50
25
Collection Interval cm
11-10-75
100
25-10-75
10
24-5-76
mg C hr-1 m-2
20
50
Incubation Interval cm
75
50
25
Collection Interval cm
1-7-76
50
8-8-76
20
6-9-76
mg C hr-1 m-2
100
50
Incubation Interval cm
75
50
25
Collection Interval cm
26-9-76
100
26-10 76
30
25-11-76

Table 9. Mean photosynthetic index, photosynthetic efficiency, and productivity efficiency by depth for the epiphyton.

	Depth interval on host stem		
	25 cm	50 cm	75 cm
Photosynthetic index	2.05	1.71	1.30
Photosynthetic efficiency	1.22	1.28	2.13
Productivity efficiency	0.09	0.21	0.35

Figure 44.
Epiphyton photosynthetic index expressed as a function of collection and incubation depth.


Carbon hr⁻¹ Chlorophyll a⁻¹
20
5
5
Incubation Interval cm
50
75
50
25
Collection Interval cm
11-10-75
25-10-75
24-5-76
Carbon hr⁻¹ Chlorophyll a⁻¹
5
5
5
Incubation Interval cm
50
75
50
25
Collection Interval cm
1-7-76
8-8-76
6-9-76
Carbon hr⁻¹ Chlorophyll a⁻¹
2
2
2
Incubation Interval cm
50
75
50
25
Collection Interval cm
26-9-76
26-10-76
25-11-76

algae from 75 cm generally yielded the highest results with the 25 cm collections comparable and the 50 cm collections notably less active. In November 1976, the 75 cm collections gave the highest photosynthetic index at each suspension depth.

5.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

Results from the three productivity relationships have been tabulated as means for the 0.25 m, 0.50 m, and 0.75 m depths respectively (Table 9). Values for the photosynthetic index appeared to decrease with depth, while those for the photosynthetic efficiency and productivity efficiency appeared to increase with depth.

Data from the 0.25 m collections taken during the May through October period of 1975 and for the same period during 1976 showed similar results. For both years a major spring peak and autumn peak were indicated for each of the three relationships. (Figure 45).

5.3. Discussion

5.3.1. Physico-chemical Parameters

Marked site to site differences in physico-chemical factors have often been presented for the littoral zone, though similarities have also been reported (Wetzel 1965, Pieczynska and Szczepanska 1966, Brown 1973a, Brown and Austin 1973b, Klarer and Hickman 1975). Aquatic macrophyte beds have been considered areas of concentrated plant standing crop acting as deposition sites for their own

Figure 45.
Seasonal distribution of the photosynthetic index, photosynthetic efficiency, and productivity efficiency for the epiphyton.

Photosynthetic Index [——]
4
2
0
M
J
S
1975
4
2
0
M
J
S
N
1976
Photosynthetic Efficiency [— — —]
0.8
0.4
0
Productivity Efficiency [— — —]

detritus as well as detritus from terrestrial runoff and phytoplankton blooms. These circumscribed regions have been shown to alter local light, temperature, oxygen, and nutrient conditions (Foerster and Schlichting 1965, Denton 1966, Klarer and Hickman 1975, Wetzel 1975, Hunter 1976). In Hastings localized silica and orthophosphate levels occurred at site EP5. The mean values were elevated when levels of 12.3 mg/l silica and 28 mg/l orthophosphate were found on 8 July, 1974, due to large phytoplankton populations collecting and senescing within the bed of Scirpus and Phragmites. However, differences among sites were often minimal; the similarities arise from the shallow, well mixed nature of the lake. Means of physico-chemical data from all sites fluctuated seasonally in a manner characteristic of temperate, eutrophic lakes (3.3.1. Physico-chemical Parameters), dependent upon and influencing in part the lakewide biota (Round 1965).

5.3.2. Species

Eight cyanophycean algae were important components of the epiphyton complex. But five of those were considered planktonic in origin (Prescott 1961, Hutchinson 1967)(6.1.2. Species). Of that group of five, Oscillatoria subbrevis and Anabaena flos-aquae were most closely correlated with incident irradiance ($r = 0.430$, $p < 0.25$, and $r = 0.800$, $p < 0.05$, respectively). Both these species showed nonsignificant, negative correlations with nutrients. The other three species in this group showed higher, significant, negative correlations with nutrients. Bicarbonate (carbon) was the

most important for Microcystis aeruginosa ($r = -0.780$, $p < 0.05$), Merismopedia tenuissima ($r = -0.390$, $p < 0.25$), and Coelosphaerium naegelianum ($r = -0.310$, $p < 0.25$). The latter species showed nonsignificant, negative correlations with light; the other two showed nonsignificant, positive correlations with light. All five of the aforementioned species had a summer peak, rather contrary to the benthic forms mentioned later. Their presence as dominant populations in the epiphyton complex resulted from the sampling technique removing an undisturbed epiphytic community; they probably originated in the phytoplankton.

The remaining blue-green dominants were benthic species common to hardwater lakes (Prescott 1961, Hutchinson 1975). Lyngbya diguetii with its filamentous nature and small cell size weighed heavily in total cell counts. It was often epiphytic upon prostrate juvenile thalli of Stigeoclonium nanum. The species showed a close negative correlation with light ($r = -0.700$, $p < 0.05$), and showed nonsignificant, positive and negative correlations with the various nutrients monitored. The Calothrix spp. contributed greatly to total cell counts also because of its filamentous form; however, it showed a very weak negative correlation with light, and relatively stronger negative correlations with nutrients, the most substantial one being against bicarbonate (carbon) ($r = -0.680$, $p < 0.10$). Yet different still were the correlations noted for Rivularia haematites, another filamentous species, with a strong positive correlation against light ($r = 0.790$, $p < 0.05$) as well as strong negative correlations against nutrients, especially bicarbonate

(carbon) ($r = -0.680$, $p < 0.10$). As different as the correlation matrices were for these three species, all exhibited major July population decreases which shaped the seasonal standing crop pattern of the epiphytic community.

Chlamydomonas spp. and Stigeoclonium nanum were the only dominants from the Chlorophyta, but they made major contributions to total cell counts. The Chlamydomonas spp. were most strongly correlated to nutrients, especially bicarbonate (carbon) ($r = -0.820$, $p < 0.05$). The Stigeoclonium nanum displayed a close negative correlation against light ($r = -0.920$, $p < 0.01$). This preference for moderate light conditions has been suggested in other studies as spring and autumn population peaks occurred (Godward 1937, Abdin 1949, Milovanovic and Petkovic 1968, Hickman and Klarer 1974). Indeed in Hastings, the mature branched form of the species did follow the spring/autumn pattern. However the inclusion of prostrate juvenile forms showed populations continued to increase spring through autumn with only a slight July plateau. And the vertical distribution in Hastings for the species showed a decided preference for the top 0.25 m. This is contrary to situations reported for other species of the same genus, where a preference was shown for deeper, dimmer lit sites (Godward 1937, Abdin 1949). Perhaps a shading of Hastings Stigeoclonium nanum by the Lyngbya diguetii species epiphytic upon it made even the 0.25 m region in summer one of moderate light conditions for the species.

Among the bacillariophycean dominants only Cocconeis placentula exhibited a summer peak. A compilation of other studies indicates

this species is capable of peaking at any time of the year (Butcher 1932b, Godward 1937, Jorgensen 1957, Castenholz 1960, Besch, et al. 1972, Hickman and Klarer 1974, 1975). The summer maximum in Hastings Lake occurred when light attenuation was greatest for the ice free period, and the vertical distribution of the species showed a preference for lower depths thus lower light. This preference for low irradiance levels has been shown in other studies (Godward 1937, McIntire 1966, Fox, et al. 1969, Tippett 1969). Because correlation coefficients were calculated for the species against incident irradiance and did not consider depth shading, the coefficient against light in Hastings was positive ($r = 0.370$, $p < 0.25$). Calculations against nutrients yielded negative coefficients, most notably against nitrate ($r = -0.430$, $p < 0.25$).

Spring and autumn peaks have been reported for Gomphonema parvulum and Rhoicosphenia curvata in several studies (Butcher 1932a, Godward 1937, Blum 1957, Jorgensen 1957, Castenholz 1960, Hufford and Collins 1976). This pattern was also noted for both species in a lake 100 km west of Hastings, where in a study on thermal effluents, it was suggested that this was a response to high summer temperatures (Hickman and Klarer 1974). However, the seasonal and vertical distributions of both species in Hastings also indicated a tendency to avoid high irradiance levels as has been suggested in other studies (Cholnoky 1929, Godward 1937, Fee 1967, Hostetter and Stoermer 1968, McIntire 1966, Klarer and Hickman 1975, Hufford and Collins 1976). Correlation coefficients calculated for both species did not offer corroboration on any of these views. For

Gomphonema parvulum the strongest coefficients were against temperature and light, but both were positive, not negative as expected ($r = 0.670$, $p < 0.10$, and $r = 0.670$, $p < 0.10$, respectively). For Rhoicosphenia curvata neither temperature nor light showed significant coefficients; negative correlations with nutrients were strongest, especially bicarbonate (carbon) ($r = -0.440$, $p < 0.25$).

Synedra acus had a restricted spring and autumn distribution, but annual maxima have been reported for each season in other studies (Godward 1937, Blum 1957, Jorgensen 1957, Castenholz 1960, Moore 1977). The species did show a strong positive correlation against incident irradiance in Hastings ($r = 0.590$, $p < 0.10$). Cyclotella meneghiniana displayed a similar positive correlation against light ($r = 0.540$, $p < 0.10$). This species likewise showed spring and autumn peaks and has been reported in other benthic studies (Patrick 1968, Moss 1969a, Coutant 1971). Although it has been commonly thought of as planktonic, particular light and temperature conditions may augment its development as an epiphyte (Patrick 1971).

Hastings Lake epiphytic Nitzschia's represent a variety of species. The genus has been reported from a wide range of conditions (Abdin 1949, Jorgensen 1957, Castenholz 1960, Patrick 1968, Evans and Stockner 1972, Koch 1975), and has shown active growth during all four seasons, reflecting its broad tolerance limits. Many of the parameters yielded significant correlation coefficients against the epiphytic Nitzschia spp., e.g. with silica,

$r = -0.490$, $p < 0.25$; nitrate, $r = -0.450$, $p < 0.25$; carbon, $r = -0.450$, $p < 0.25$; orthophosphate, $r = -0.410$, $p < 0.25$; temperature, $r = 0.42$, $p < 0.25$; and light, $r = 0.480$, $p < 0.25$.

The algal divisions represented a composite level of species' seasonal and vertical responses to physico-chemical conditions. The three algal divisions displayed tendencies for preferred depths, even though data was collected from a rather narrow range of depths. Other studies using both artificial as well as natural substrates have shown general distributions over deeper intervals (Cannon, et al. 1961, Evans and Stockner 1972). Diatom numbers have been found increasing with depth, indicating an apparent aversion to high light levels, as may have occurred in Hastings Lake (Godward 1937, Abdin 1949, Tippett 1969). However, the distribution could indicate relatively weaker attachment mechanisms of diatoms in conjunction with wave action near the surface (Young 1945, Knudson 1957, Fox, et al. 1969). Chlorophycean algae have been found nearer the water surface, preferring higher light (Godward 1937, Abdin 1949, Brown 1976). In Hastings Lake there is a preference for the top 50 cm, but a decrease in the upper 25 cm may represent attachment capabilities. The distribution of epiphytic cyanophycean algae suggests a positive response to high irradiance as noted in other studies (Abdin 1949, Brown 1976), an ability to remain attached in considerable wave action, and an ability to survive exposure as water levels fluctuate (Hutchinson 1975).

Seasonally the Cyanophyta and the Chlorophyta have been associated with high temperatures (Godward 1937, Cairns 1956,

Coutant 1971, Cairns, et al. 1972), but in Hastings Lake rapid spring increases formed peaks, or plateaus, for both divisions, which subsequently generated increases to autumn maxima before winter minima. Also, notable in Hastings Lake was the interplay of the percentage contribution each division made to total community cell numbers. These peaks of community related activity occurred over broad temperature and irradiance regimes. Among nutrients, dissolved silica, nitrate, and orthophosphate showed some positive association with proportionate Chlorophyta peaks, but the relationship most persistent through all four seasons was between peak alkalinity and peak percent Chlorophyta. The Cyanophyta then made its greatest percent contributions to the community when the predominant carbon source reflected in total alkalinity was relatively lower. They may possess a physiological advantage in processing available carbon sources (King 1970, Shapiro 1973, Colman and Coleman 1978). Apparent competition exists between the two divisions, but contrapunctual populations provide a harmonious community response to variable carbon sources.

Spring and autumn increases in diatom numbers and in their abundance relative to total cell numbers is not uncommon (Godward 1937, Jorgensen 1957, Hickman and Klarer 1974). Temperature has been considered the major controlling factor (Cairns 1956, Patrick, et al. 1969, Coutant 1971, Patrick 1971). Calcium, manganese, pH, and biological interactions have been also cited as important (Patrick 1968, Patrick, et al. 1969). In Hastings Lake, diatom growth commenced under ice and snow in the early spring, indicating

a response to increasing irradiance levels. Knudson (1957) suggests this is to be expected as epiphytes are able to position themselves to obtain the most favorable irradiance levels. Thus low to moderate irradiance and temperature favored development of the epiphytic diatoms.

Diversity indices represent a community response to physico-chemical and biotic interactions (Johnson, et al. 1968, Dickman 1969, Goulden 1969, Slobodkin and Sanders 1969). Decreasing diversity is associated with increasing environmental stress (Odum 1971). Diversity of the epiphyton in Hastings Lake increased with depth, even though no drastic physico-chemical factor, except light levels appeared to have changed. In fact, seemingly advantageous light conditions occurred in the 25 cm region. But, as high standing crops at 25 cm increased, a multi-storied layering was initiated (e.g., Lyngbya diguetii extended above prostrate juvenile Stigeoclonium nanum with diatoms interspersed among the matrix). This layering has been noted in other epiphytic studies (Allanson 1973, Brown 1976), and could effect availability of nutrients and light within the epiphytic microcosm (Allen 1971, Allanson 1973) and create stresses, thus lowered diversities, at the 25 cm level.

With regard to seasonal patterns of diversity, Eminson (1978) has suggested epiphytes may increase in diversity spring through autumn. However, in this study spring diversity was high with conditions allowing influx of many species onto old host stems somewhat ice stripped by harsh winters, and onto new stems freshly growing. As the seasons progressed and standing crops increased,

the competition for nutrients would increase, as would competition for decreasing light, and perhaps most importantly the competition for decreasing space. Species with adaptive attachment mechanisms and complementary physiological adaptations then outcompete other species. Competition within the microcosm may be revealed by the community's diversity responses since as standing crop increased, diversity decreased, even though there was no apparent increase in environmental stress, a situation noted by Brown (1973b) for algae colonizing glass slides.

5.3.3. Standing Crop

Large site to site variations in standing crop for the epiphyton have been reported (Allen 1971, Hickman and Klarer 1975, Komarkova and Komarek 1975, Kowalczewski 1975). But in Hastings whatever site variations there may have been in physico-chemical parameters, the resultant changes in epiphytic standing crop were relatively even lakewide. Cell counts provided a reasonable estimate of community size (Lund, et al. 1958), and in addition, provided background data for individual species. Although the presence of smaller species tended to overemphasize and the presence of larger species tended to underemphasize total counts (Hickman 1973, Klarer and Hickman 1975), no immediate problems were evident. Chlorophyll a provided another estimate of community size, and in addition, expressed more directly the physiological relationship between community photosynthesis and the environment. Again problems could occur as chlorophyll a can vary per species unit, and

thus, its proportion from one species to another (Sargent 1940, Tippett 1969, Hillbricht-Ilkowska, et al. 1972, Hickman 1976b). However Hastings chlorophyll a and cell counts showed similar seasonal patterns ($r = 0.840$, $p < 0.01$) suggesting the above problems may have been counterbalanced within the community by interacting populations.

Vertical distribution studies of epiphyte standing crops have reported maxima at various depths (Pieczynska 1968, Allen 1971, Hillbricht-Ilkowska, et al. 1972). Maxima in this study were predominantly nearer the surface, presumably because of higher light. Exceptions occurred especially in the spring since the epiphytic populations that survived the winter were retained on the lower portions of old stems whose upper portions had been scoured clean by the ice. Moreover, new growing stems also offered a substratum from the bottom upwards as they matured. Thus in May and June 1975 and 1976, the largest standing crops were formed in the 50 and 75 cm regions.

Seasonal standing crop changes were similar to those found by Klarer and Hickman (1975) who postulated that a relatively late ice break up prevents the development of a large spring maximum, thereby modifying the comparative amplitudes of the spring and autumn maxima. In Hastings cell count data and chlorophyll a data yielded differing correlation interpretations. Total cell counts showed the highest coefficient against light ($r = -0.750$, $p < 0.05$); whereas, chlorophyll a displayed its highest coefficient against bicarbonate (carbon) ($r = -0.590$, $p < 0.10$) with a negative, but nonsignificant,

correlation against light. But both major correlations reflect the relatively small spring peak and the large autumn peak from the standpoint of light and nutrients as well as the previously mentioned ice action.

5.3.4. Productivity

Epiphytic productivity generally decreased with depth as standing crop and irradiance levels decreased except in November 1976, when a large standing crop at 25 cm was less productive than a smaller one at 75 cm. However, the overall importance of irradiance levels was seen during May and July 1976, when productivity decreased with depth even though standing crop increased.

Among epiphyte seasonal productivity studies on natural substrates a good correspondence is usually noted between productivity and chlorophyll _a_ standing crop, such that spring and autumn activity appear to be characteristic (Hickman 1971b, 1974, Hickman and Klarer 1975, Komarkova and Komarek 1975, Kowalczewski 1975, Sheldon and Boylen 1975). Comments relating the seasonal aspects of epiphyte production to other factors have not been elaborate; general references to light quality and quantity, and temperature have most often been made (Cannon, _et al_. 1961, Pieczynska 1968, Hickman 1971b, 1974, Hickman and Klarer 1975, Komarkova and Komarek 1975). Nutrient cycles have not been considered important, perhaps because of adequate nutrient concentrations being recycled at the microcosm level (Allen 1971, Harlin 1975, Thorhaug 1975). Additions of nitrogen and phosphorus

to epiphyte incubations have not resulted in marked productivity increases (Stockner and Evans 1974). However, as carbon is the major standing crop constituent, productivity may follow overall carbon. Indications of such a situation have been reported from an oligotrophic lake in which spiked epiphyte incubations showed no positive reaction to PO_4, NO_3, $PO_4 + NO_3$, NH_4, SiO_2, or SO_4 additions, but did react positively to bicarbonate additions (Sheldon and Boylen 1975). In addition to being the major carbon source between pH 7 and 10, bicarbonate is a measure of weak acid salts and may be indicative of overall nutrient status (Lund 1957, Moss 1969b). This assumption has been used to propose a positive correspondence between increasing bicarbonate levels and increasing standing crop and productivity in other benthic algal communities where specific nutrients (e.g. PO_4, or NO_3) may be supplemented from substrates (Moss 1969b, Hickman 1971a, 1978). Indeed, in relation to the above, Hasting epiphytic productivity showed its highest correlation coefficients against standing crop chlorophyll a (1975, $r = 0.850$, $p < 0.01$, 1976, $r = 0.810$, $p < 0.01$) and carbon (1975, $r = 0.900$, $p < 0.01$, 1976, $r = 0.830$, $p < 0.01$). Spiking techniques in the epiphyton of eutrophic Hastings may follow the results from oligotrophic lakes (Sheldon and Boylen 1975).

5.3.5. Cross Incubation Studies

The cross incubation studies presented the relative metabolic activity of the various algal populations. The seasonal patterns of the photosynthetic indices suggested an interplay of "sun and shade"

adapted epiphytic algae (Allen 1971, Jones and Adams 1982). The sun adapted algae at 25 cm were the most metabolically active group during the spring when increasing irradiance and photoperiods are important. Then as summer commenced both the sun adapted algae at 25 cm and the shade adapted ones at 75 cm exhibited comparable active responses. As autumn and winter approached a sharp decline in the activity of the sun adapted algae occurred, and the shade adapted forms became the most active.

5.3.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

References to the three productivity relationships are virtually nonexistent.

On a seasonal basis bicarbonate (carbon) showed positive correlations with the photosynthetic index (1975, $r = 0.900$, $p < 0.01$; 1976, $r = 0.830$, $p < 0.05$) and with the photosynthetic efficiency (1975, $r = 0.680$, $p < 0.10$; 1976, $r = 0.690$, $p < 0.10$). The productivity efficiency was most closely correlated with temperature (1976, $r = -0.670$, $p < 0.25$).

Overall the populations from 25 cm yielded the highest photosynthetic index and so showed the greatest metabolic activity. But the populations from 75 cm showed the highest photosynthetic efficiency and productivity efficiency.

6. COMPARISON OF ALGAL COMMUNITIES

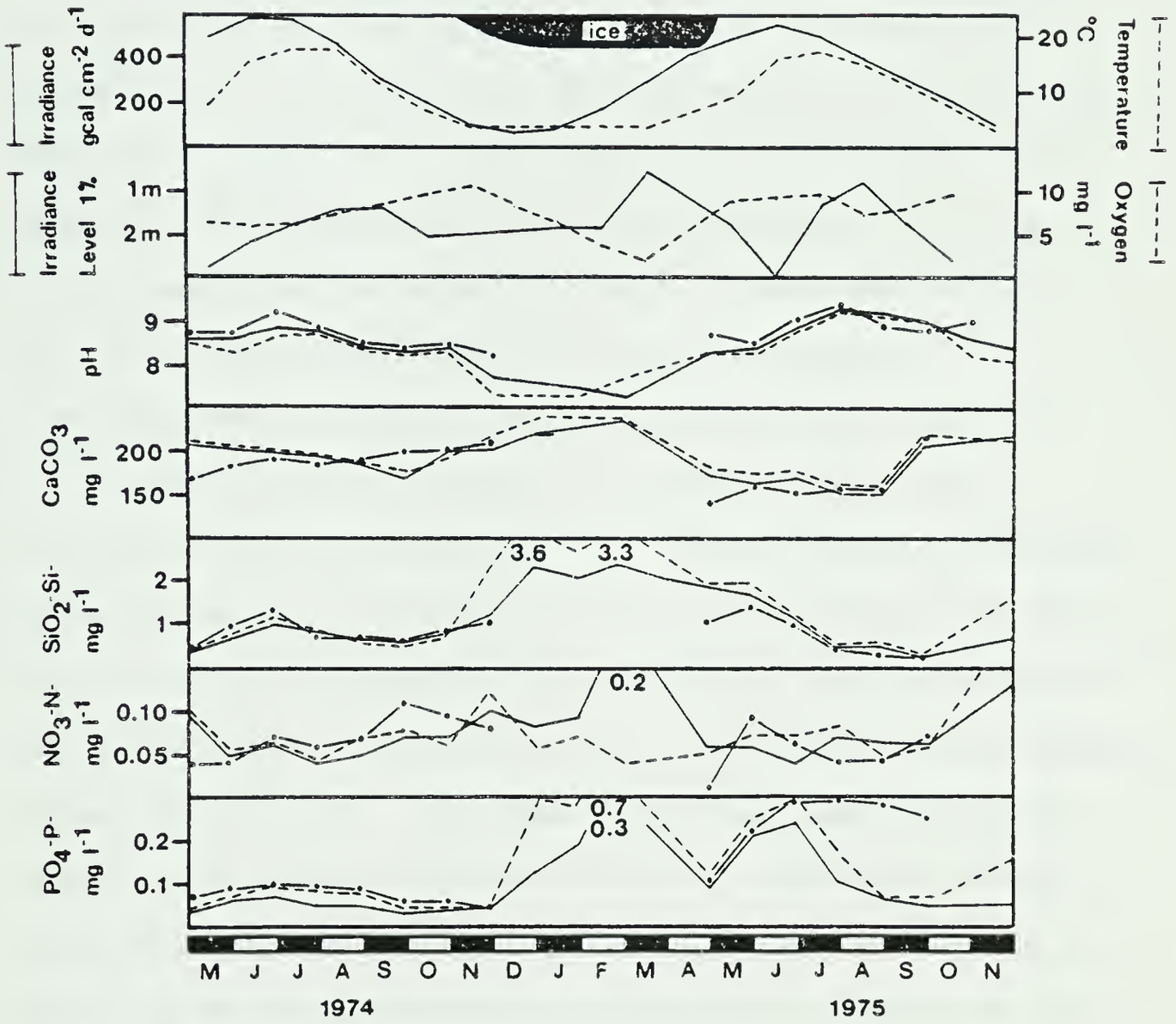
6.1. Results

6.1.1. Physico-chemical Parameters

The relative amount of light impinging upon the three algal communities under study was indicated by the depth of the 1% photosynthetically active radiation level (Figure 46). The penetration of available surface irradiance into the water was greatest in spring and autumn; the annual mean was 2 m. Therefore the mean depth of the euphotic zone for the phytoplankton and the epipelon was at 2 m. However, light striking the lake surface within macrophyte stands was approximately 55% of that striking the surface on open water portions of the littoral zone and the pelagial zone. The mean depth of the euphotic zone then for the epiphyton was closer to 1 m. Monthly means of incident irradiance showed a tenfold increase from December to June, but the fluctuations were seasonally smooth for all three algal communities (Figure 46).

The vertical distribution of temperature generally showed isothermal conditions during the ice free period and inverse stratification during the winter under ice and snow cover (3.2.1. Physico-chemical Parameters, 4.2.1. Physico-chemical Parameters, 5.2.1. Physico-chemical Parameters). Thus a seasonal graph of mean lake temperatures reached maxima near 20 °C in summer and near 2 °C in winter (Figure 46). In winter ice was formed to a depth of approximately 75 cm and varying amounts of snow cover were present. A temperature lag behind incident irradiance from mid winter to mid

Figure 46.
Seasonal distribution of surface irradiance, depth of 1% surface irradiance, temperature, and oxygen; seasonal distribution of pH, mg/l calcium carbonate, mg/l silica, mg/l nitrate, and mg/l orthophosphate for the phytoplankton (_____), the epipelon (-----), and the epiphyton (__.__.).


Irradiance
Irradiance
Level 1%
pH
$CaCO_3$ mg l^{-1}
SiO_2-Si- mg l^{-1}
NO_3-N- mg l^{-1}
PO_4-P- mg l^{-1}
gcal cm^{-2} d^{-1}
ice
1m
2m
400
200
9
8
200
150
2
1
0.10
0.05
0.2
0.1
3.6
3.3
0.2
0.7
0.3
20
10
°C
Temperature
10
5
mg l^{-1}
Oxygen
M J J A S O N D J F M A M J J A S O N
1974
1975

summer was noted. But relatively quick heating in the spring and cooling in the autumn were evident.

Percent oxygen saturation showed some stratification in the pelagial and the littoral zones (3.2.1. Physico-chemical Parameters, 5.2.1. Physico-chemical Parameters) such that oxygen levels were often higher near lake surface for the three algal communities. The epipelon as a benthic community distributed over the 0 to 7 m depths was notably subjected to this vertical oxygen gradient. But relative seasonal fluctuations were similar for all three communities, and a mean lake oxygen graph showed a trend toward highest oxygen in spring and autumn with winter concentrations considerably lower than summer ones (Figure 46).

A depth distribution for pH was noted over the 0 to 7 m interval of the phytoplankton (3.2.1. Physico-chemical Parameters). A general decrease with depth occurred. Presentations of pH from each of the three communities indicated values from the epiphyton > the phytoplankton > the epipelon for the May through October periods (Figure 46, Table 10). All communities showed summer maxima and winter minima within a range of 7.3 to 9.3. Alkalinity tended to increase with depth over the 0 to 7 m depth interval. Alkalinity values for May through October data showed mg/l calcium carbonate for the epipelon > the phytoplankton > the epipelon (Figure 46, Table 10). Concentrations ranged from 146 to 243 mg/l and showed autumn minimn and winter maxima for values from the phytoplankton and epipelon. In the epiphyton spring minima and winter maxima were shown.

Table 10. Means and standard deviations for May through October chemistry data of the phytoplankton, epipelon, and epiphyton.

	Phytoplankton	Epipelon	Epiphyton
pH			
1974	8.60 ± 0.20	6.50 ± 0.20	8.70 ± 0.30
1975	8.90 ± 0.40	8.80 ± 0.40	8.90 ± 0.30
$CaCO_3$ mg/l			
1974	195.00 ± 13.00	196.00 ± 11.00	188.00 ± 11.00
1975	173.00 ± 20.00	180.00 ± 18.00	168.00 ± 26.00
SiO_2-Si mg/l			
1974	0.68 ± 0.24	0.67 ± 0.27	0.71 ± 0.37
1975	0.97 ± 0.70	1.03 ± 0.74	0.76 ± 0.47
NO_3-N mg/l			
1974	0.06 ± 0.02	0.07 ± 0.02	0.07 ± 0.02
1975	0.06 ± 0.01	0.06 ± 0.01	0.06 ± 0.01
PO_4-P mg/l			
1974	0.05 ± 0.02	0.07 ± 0.03	0.08 ± 0.02
1975	0.13 ± 0.08	0.15 ± 0.11	0.25 ± 0.09

The range of silica from all three communities was 0.25 to 3.60 mg/l. Relative concentrations among communities varied during the May to October period but a tendency for higher levels in the epipelon were noted (Figure 46, Table 10). Overall spring silica lows were associated with high diatom populations in the phytoplankton (Figure 47). As planktonic diatom populations rapidly decreased, the increase in silica was dampened somewhat by increasing epipelic diatom populations which were of relatively minor proportions on a lakewide basis. Silica showed its minor summer peak when epipelic diatoms subsided. This peak was muted by increasing epiphytic diatom populations and a pulse of planktonic diatoms. The major silica decrease in autumn can be attributed to large diatom populations in the epiphyton. Early winter diatom populations in all communities were low, and silica levels increased to mid-winter maxima only to decrease as late winter epipelic diatom populations increased. This complex negative relationship among lakewide silica levels and diatom populations from three algal communities can be empirically approximated for predictive purposes by a linear equation. Using transformed data pairs, the reciprocal of silica concentrations and the base ten logarithm of total lake diatoms, a linear regression line can be created which has a slope near one and a y intercept near zero ($r = 0.840$, $p > 0.01$, $y = 1.06 x + 0.19$) (Figure 48).

Nitrate and orthophosphate in Hastings showed some interesting vertical distributions over the 0 to 7 m interval (3.2.1. Physico-chemical Parameters). Both increased with depth during ice

Figure 47.
Seasonal distribution of diatom populations from the phytoplankton (_____), the epipelon (-----), and the epiphyton (. . . . .) along with that of mg/l silica (_____).

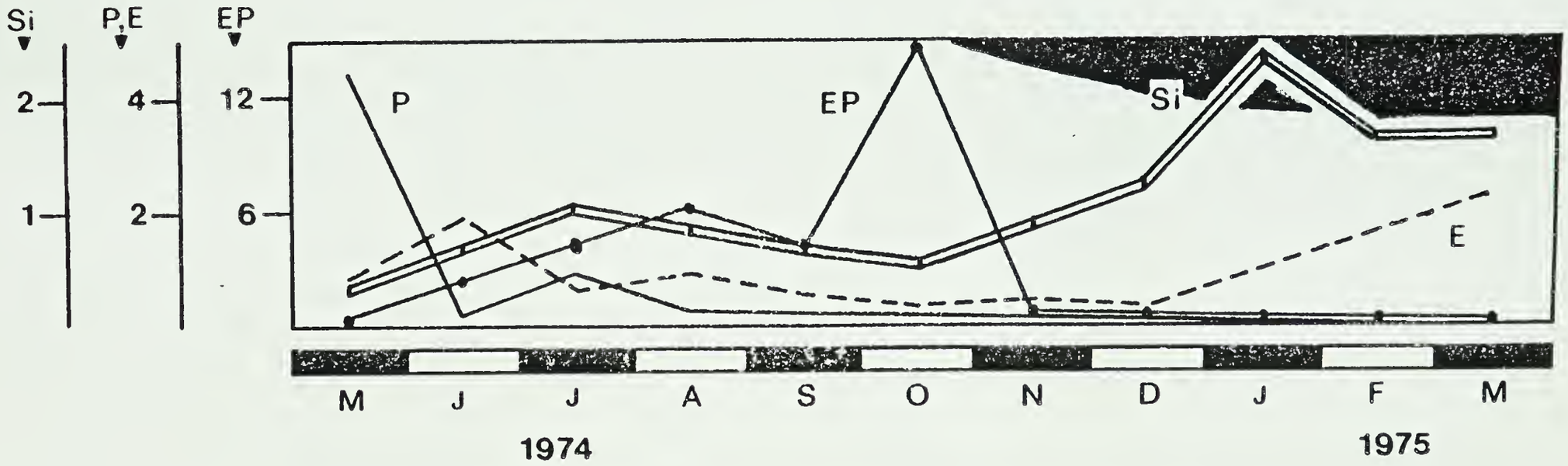
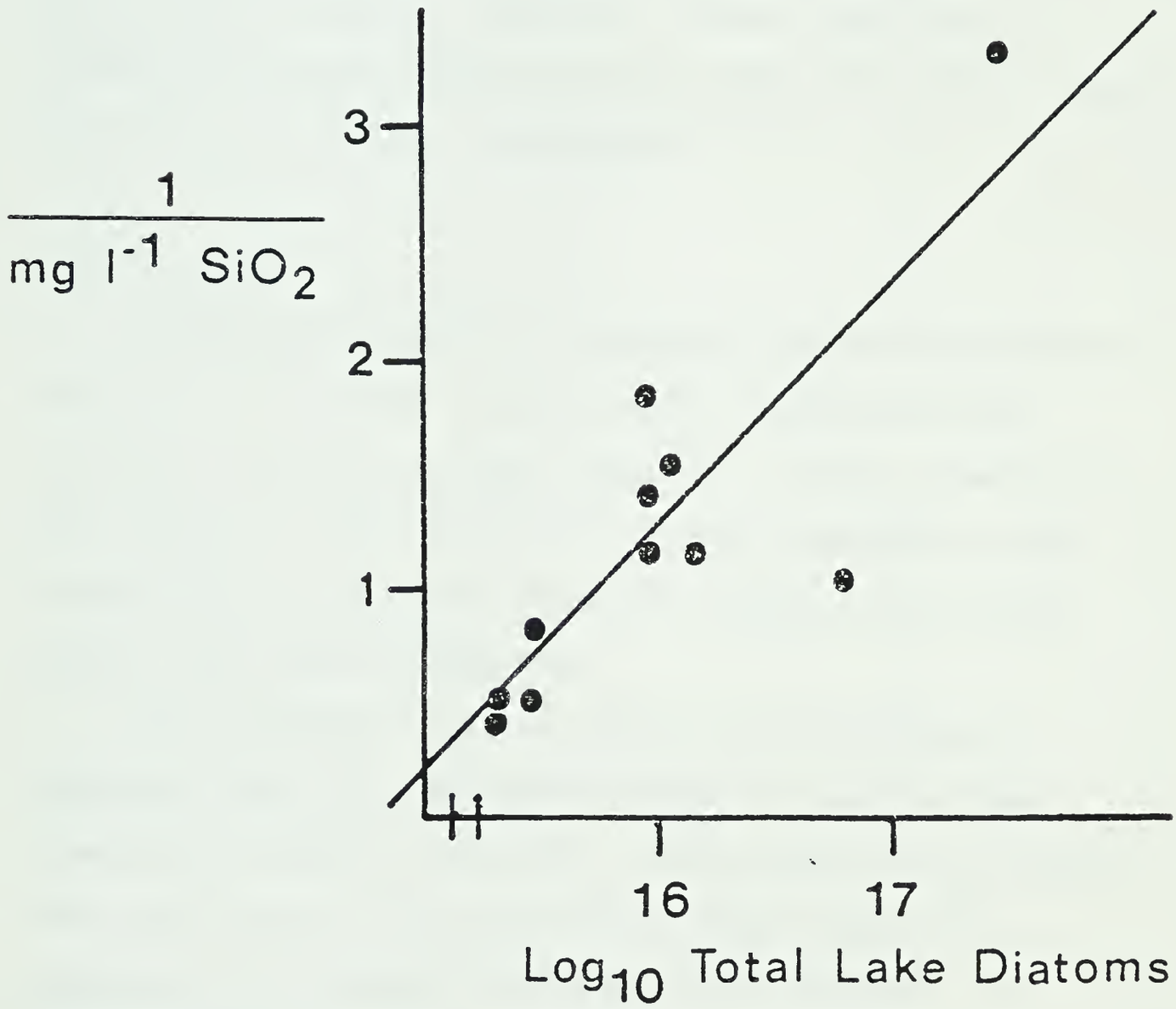

Si
P,E
EP
2
1
4
2
12
6
P
EP
Si
E
M
J
J
A
S
O
N
D
J
F
M
1974
1975

Figure 48.
Log_{10} total lake diatoms
graphed against the reciprocal
of mg/l silica.


1
mg l-1 SiO2
3
2
1
16
17
Log10 Total Lake Diatoms

free seasons, but only orthophosphate did so under winter ice and snow; nitrate decreased with depth. The relative amounts of nitrate available among communities was not consistent, but winter maxima and summer peaks occurred within a range of 0.01 to 0.25 mg/l for all communities (Figure 46, Table 10). Orthophosphate concentrations showed values for the epiphyton > epipelon > phytoplankton (Figure 46, Table 10). Seasonal data from all communities displayed winter maxima and summer peaks within a range of 0.03 to 0.66 mg/l for orthophosphate.

6.1.2. Species

A total of 169 species were identified from the phytoplankton, epipelon, and epiphyton in Hastings Lake. Forty species were recorded as numerical dominants (Table 11). Of these, twenty-one were dominant in one community and of little consequence in other communities. The remaining nineteen were dominant and at least common in more than one community.

Seven cyanophycean species did show such intercommunity importance (Table 11). These were graphed on a seasonal basis community by community (Figure 49). Taking special note of the year when each of these species showed their largest populations, patterns of intercommunity development can be discerned. For Anabaena flos-aquae, Coelosphaerium naegelianum, and Merismopedia glauca dominant populations occurred in all three communities with the exception of the latter species only being common in the epiphyton (Table 11). For each of the aforementioned species,

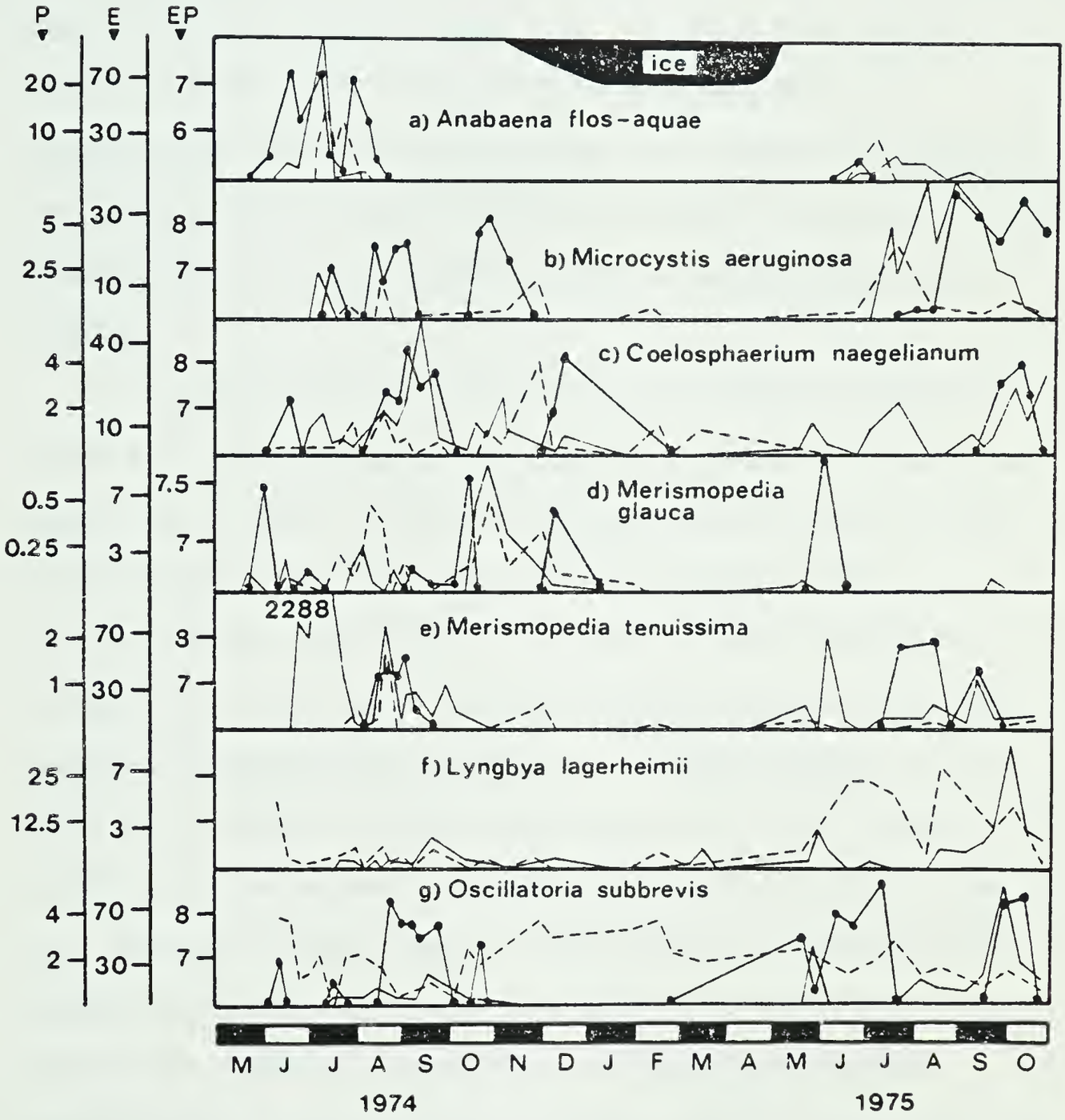
Table 11. Dominant algae from the phytoplankton (P), epipelon (E), and epiphyton (EP). Dominant ≥ 20% of the total community cell counts on any given sampling date, Common ≥ 1%, Present < 1%.

	P	E	EP
Cyanophyta:			
Anabaena circinalis Rabenhorst	D	P	P
Anabaena flos-aquae (Lyng.) De Brebisson	D	D	D
Aphanizomenon flos-aquae (L.) Ralfs	D	-	P
Calothrix species C.A. Agardh	-	-	D
Coelosphaerium neagelianum Unger	D	D	D
Gomphosphaeria lacustris v. compacta Lemmermann	D	P	P
Lyngbya diguetii Gomont	-	-	D
Lyngbya lagerheimii (Moebius) Gomont	D	D	-
Merismopedia glauca (Ehr.) Naegli	D	D	C
Merismopedia tenuissima Lemmermann	D	D	D
Microcystis aeruginosa (Kutz.) Elenkin	D	D	D
Oscillatoria subbrevis Schmidle	D	D	D
Rivularia haematites (D.C.) C.A. Agardh	-	-	D
Chlorophyta:			
Ankistrodesmus falcatus (Corda) Ralfs	D	C	P
Botryococcus sudeticus Lemmermann	D	-	P
Chlamydomonas spp. Ehr.	D	D	D
Chlorella vulgaris Beverinck	D	D	P
Crucigenia quadrata Morren	D	D	P
Dictyosphaerium pulchellum Wood	D	D	P
Gonium sociale (Dju.) Warming	D	C	P
Micractinium pusillum Fresenius	D	-	P
Pandorina morum (Mull.) Bory	D	P	P
Pediastrum boryanum (Turp.) Meneghini	C	D	C
Sphaerocystis schroeteri Chodat	D	P	P
Stigeoclonium nanum Kutz.	P	P	D
Bacillariophyta:			
Achnanthes sp. Bory	-	D	P
Cocconeis placentula Ehr.	-	P	D
Cyclotella meneghiniana Kutz.	C	C	D
Gomphonema parvulum Kutz.	-	P	D
Navicula cryptocephala Kutz.	P	D	C
Navicula gracilis Ehr.	-	D	-
Navicula hungarica v. capitata (Ehr.) Cleve	-	D	-
Nitzschia spp. Hassall	D	D	D

(Continuation of Table 11)

Nitzschia gracilis Hantzsch	-	D	-
Nitzschia palea (Kutz.) W. Smith	D	D	P
Rhoicosphenia curvata (Kutz.) Grunow	P	P	D
Stephanodiscus hantzschii Grunow	D	C	P
Synedra acus Kutz.	P	P	D
Euglenophyta:			
Trachelomonas granulosa Playfare	C	D	-
Cryptophyta:			
Rhodomonas minuta Skuja	D	P	P

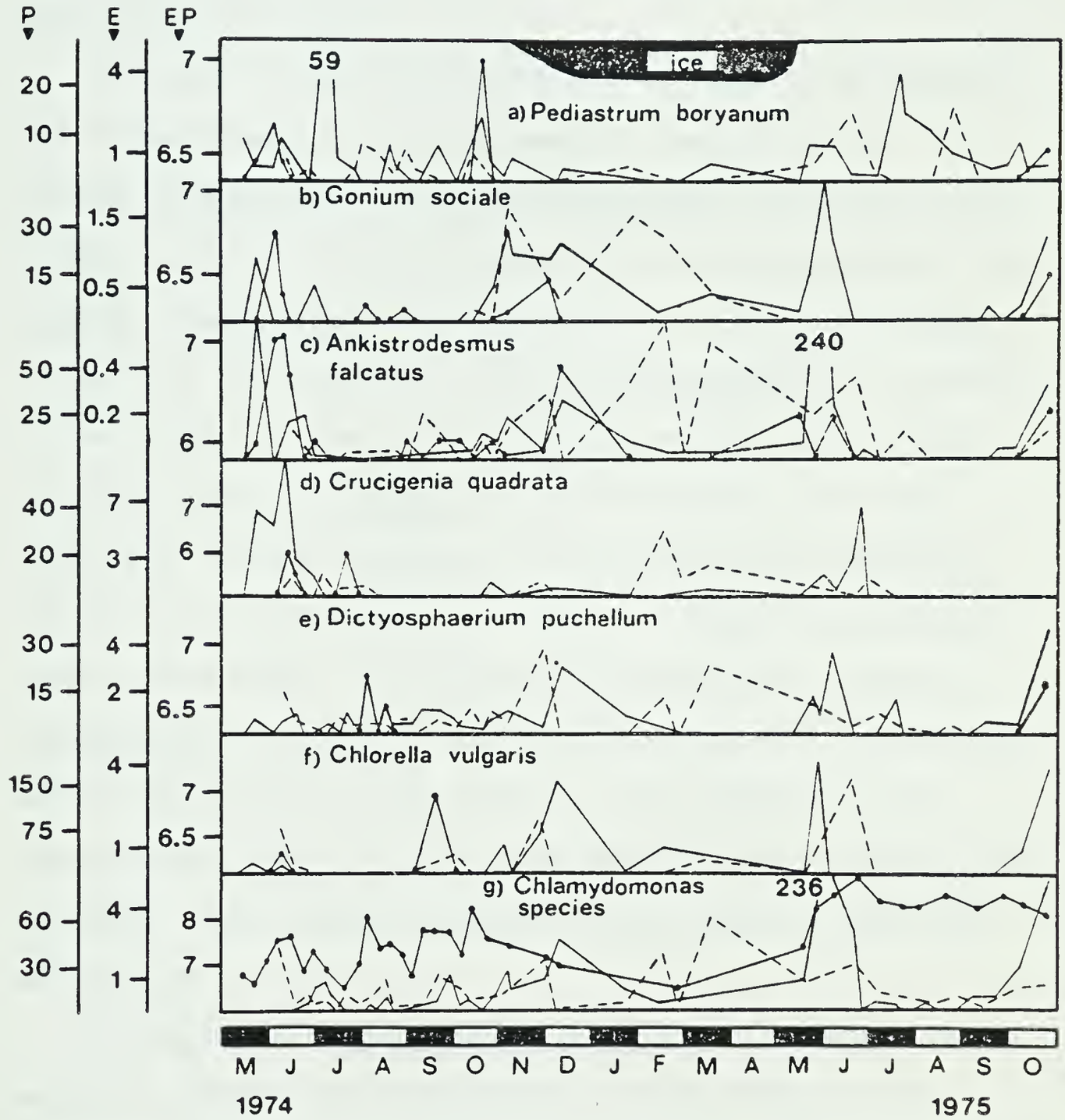
Figure 49.
Seasonal distribution of
Anabaena flos-aquae, *Microcystis aeruginosa*, *Coelosphaerium naegelianum*, *Merismopedia glauca*, *Merismopedia tenuissima*, *Lyngbya lagerheimii*, and
Oscillatoria subbrevis
for the phytoplankton (____),
the epipelon (-----), and the
epiphyton (._____.).


P
E
EP
ice
a) Anabaena flos-aquae
b) Microcystis aeruginosa
c) Coelosphaerium naegelianum
d) Merismopedia glauca
2288
e) Merismopedia tenuissima
f) Lyngbya lagerheimii
g) Oscillatoria subbrevis
M J J A S O N D J F M A M J J A S O
1974
1975

populations peaks occurred first in epiphyton, then phytoplankton, then epipelon (Figure 49). For Microcystis aeruginosa, Oscillatoria subbrevis, and Lyngbya lagerheimii dominant populations occurred in all three communities with the exception of the latter species being absent from the epiphyton (Table 11). For these three species, population peaks first occurred in the epipelon, then the phytoplankton and/or epiphyton (Figure 49). Dominant Merismopedia tenuissima populations were found in all three algal communities and peaked first in the phytoplankton, then in the epiphyton and/or epipelon.

Seven chlorophycean species showed intercommunity importance (Table 11). Whereas most of the cyanophycean species formed large populations in one of the benthic communities first, most of the chlorophycean species were shown initiating peaks in the phytoplankton and then peaks in the epipelon and/or epiphyton (Figure 50). Such species included Chlorella vulgaris, Crucigenia quadrata, Dictyosphaerium pulchellum, and Gonium sociale, all of which were dominants in the phytoplankton and at least common in the epipelon, but not present in great numbers in the epiphyton (Table 11). For each of those species, large epipelic populations were notable during the winter months as populations in the other two communities decreased (Figure 50). For Pediastrum boryanum, phytoplanktonic populations also preceeded benthic populations, but the species was a dominant in the epipelon, and common in the epiphyton and phytoplankton; it was in the latter two communities that important winter populations were found. The various

Figure 50.
Seasonal distribution of
Pediastrum boryanum,
Gonium sociale,
Ankistrodesmus falcatus,
Crucigenia quadrata, *Dictyosphaerium*
pulchellum, *Chlorella vulgaris*,
and
Chlamydomonas
species for the phytoplankton
(____), epipelon (-----),
and epiphyton (.____.).


P
E
EP
ice
59
240
236
a) Pediastrum boryanum
b) Gonium sociale
c) Ankistrodesmus falcatus
d) Crucigenia quadrata
e) Dictyosphaerium puchellum
f) Chlorella vulgaris
g) Chlamydomonas species
M J J A S O N D J F M A M J J A S O
1974
1975

Chlamydomonas species as a composite showed more, or less, simultaneous peaks in all three communities, and was a dominant in all three communities (Figure 50, Table 11); during winter, populations decreased overall in the phytoplankton and epiphyton and increased in the epipelon.

Four bacillariophycean species were dominants in one community and at least common in a second community (Table 11). For Cyclotella meneghiniana, Navicula cryptocephala, and Nitzschia spp., benthic population peaks preceeded peaks in the phytoplankton. The Cyclotella meneghiniana was a dominant in the epiphyton and common in the other two communities. Navicula cryptocephala was a dominant in the epipelon, common in the epiphyton, and only rarely present in the phytoplankton. Nitzschia spp. were dominants in all three communities. Winter populations in the epipelon were especially important with populations in the other two communities decreasing greatly at that time. The remaining bacillariophycean alga was Stephanodiscus hantzschii; large phytoplankton populations preceeded benthic populations for this species. It was dominant in the phytoplankton, common in the epipelon and only rarely present in the epiphyton. Again, epipelic populations were especially important during winter.

The euglenophyte Trachelomonas granulosa was a dominant in the epipelon, common in the phytoplankton, and not present in the epiphyton (Table 11). Epipelic peaks tended to occur first, then phytoplanktonic and epiphytic peaks (Figure 51).

The percent composition of total counts was often highest for

Figure 51.
Seasonal distribution of
Trachelomonas granulosa,
Cyclotella meneghiniana,
Stephanodiscus hantzschii,
Nitzschia species, and
Navicula cryptocephala
for the phytoplankton (____),
epipelon (-----), and
epiphyton (.____.).

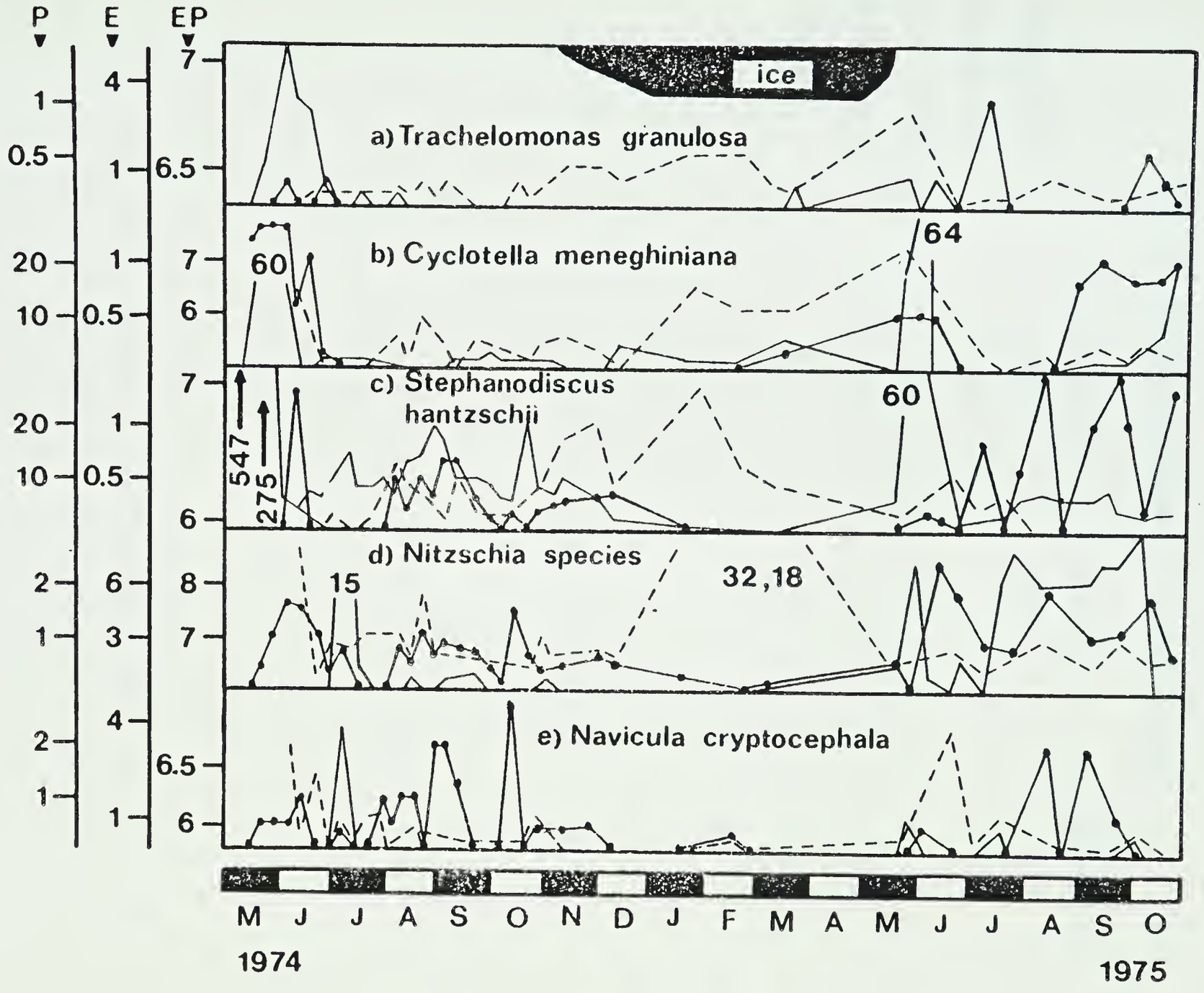

P
E
EP
ice
a) Trachelomonas granulosa
b) Cyclotella meneghiniana
60
64
c) Stephanodiscus hantzschii
547
275
60
d) Nitzschia species
15
32,18
e) Navicula cryptocephala
M J J A S O N D J F M A M J J A S O
1974
1975

Table 12.

Percent composition of algal divisions in the phytoplankton, epipelon, and epiphyton.

	Phytoplankton	Epipelon	Epiphyton
Cyanophyta	59%	81%	56%
Chlorophyta	39%	5%	41%
Bacillariophyta	<1%	12%	3%
Euglenophyta	<1%	2%	<1%
Others	<1%	<1%	<1%

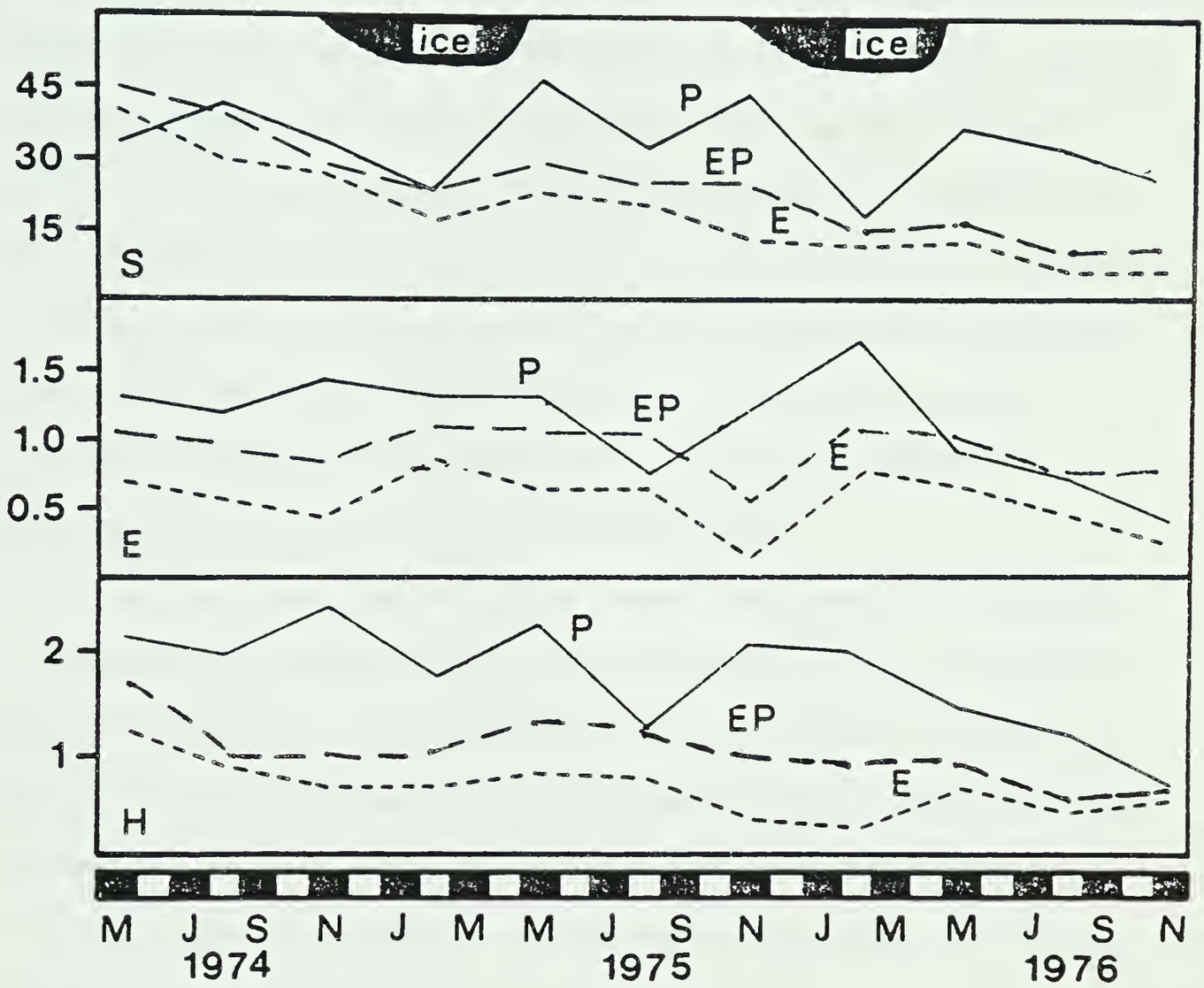
the Cyanophyta in all three communities (Table 12). The Chlorophyta provided the major counterpoint in the phytoplankton and epiphyton (3.2.2. Species, 5.2.2. Species), but was not as important in the epipelon where the Bacillariophyta was of greater note (4.2.2. Species). Diatoms were of some importance in the epiphyton (5.2.2. Species), and the euglenophytes were so in the epipelon (4.2.2. Species).

Overall species interrelationships were represented by species richness (S), evenness (E), and diversity (H) for the respective communities. Vertical distributions showed no distinct profile for the phytoplankton (3.2.2. Species); for the epipelon diversity decreased with depth (4.2.2. Species), while for the epiphyton diversity increased with depth (5.2.2. Species). The seasonal responses of all three communitie suggested high spring indices decreased through summer to low autumn/winter indices; however, the evenness of species tended to increase in winter for each community (Figure 52). The phytoplankton generally had the highest values for the three indices, followed by the epiphyton, then the epipelon (Figure 52).

6.1.3. Standing Crop

Vertical distributions for standing crop among the three algal communities showed the profile for the phytoplankton and the epipelon to be even to irregular (3.2.3. Standing Crop, 4.2.3. Standing Crop), while that of the epiphyton decreased with depth (5.2.3. Standing Crop).

Figure 52.
Seasonal distribution of species richness S, species evenness E, and Shannon's diversity H for the phytoplankton (_____), epipelon (-----), and epiphyton (._____.).


ice
ice
45
30
15
P
EP
E
S
1.5
1.0
0.5
P
EP
E
E
2
1
P
EP
E
H
M J S N J M M J S N J M M J S N
1974
1975
1976

Standing crop data from 0 m was averaged over the ice free seasons for each community (Table 13). Thus based on per m^3 units, the phytoplankton yielded the largest standing crop. The epiphyton mean values based on per m^2 host stem units were less, but still substantial as 1975 epiphytic standing crop approached that of the phytoplankton. Furthermore, within the littoral zone 0 to 1 m depth interval, where approximately 200 emergent macrophyte host stems per m^2 were common, the standing crop per m^2 lake surface area was greatest for the epiphyton, not the phytoplankton. Standing crop for the epipelon was relatively small in either case. On a total lake basis over the three year period the phytoplankton accounted for 75% of the total lake standing crop, while the epiphyton contributed 23%, and the epipelon 2%. Total lake summations decreased year to year from 1974 through 1976.

Seasonal data from all three communities created a composite seasonal pattern for total lake standing crop during the ice free period (Figure 53). The seasonal pattern for total lake standing crop closely correlated with the seasonal pattern for phytoplankton standing crop ($r = 0.990$, $p > 0.005$). Still in the late spring and in the autumn the epiphyton contributed more to total lake biomass than did the phytoplankton.

Interesting qualitative interactions among the three communities were shown by seasonal standing crop data based on 0 m samples from 1975 (Figure 54). During May and June, a series of spring peaks occurred as the phytoplankton, then the epipelon, and then the epiphyton peaked. During July and August, a progression of

Table 13. Standing crop chlorophyll a for each algal community at 0 m, in the 0-1 m littoral zone, and on a total lake basis.

Standing crop mg chlorophyll a at 0 m	May-Oct. 1974	May-Oct. 1975	May-Oct. 1976
Phytoplankton m^{-3} water column	75	51	117
Epipelon m^{-2} sediment surface	6	2	2
Epiphyton m^{-2} host stem	19	43	28

Standing crop mg chlorophyll a in littoral zone 0-1 m depth interval	May-Oct. 1974	May-Oct. 1975	May-Oct. 1976
Phytoplankton m^{-2}	75	51	117
Epipelon m^{-2}	6	2	2
Epiphyton m^{-2}	179	405	264

Standing crop kg chlorophyll a in lake total	May-Oct. 1974	May-Oct. 1975	May-Oct. 1976
Phytoplankton	1300	865	722
Epipelon	52	13	13
Epiphyton	176	403	260
Summation	1528	1281	995

Figure 53.
Seasonal distribution of ln mg chlorophyll a for total lake phytoplankton (____), total lake epipelon (-----), total lake epiphyton (.____.), and total lake summation (_____).

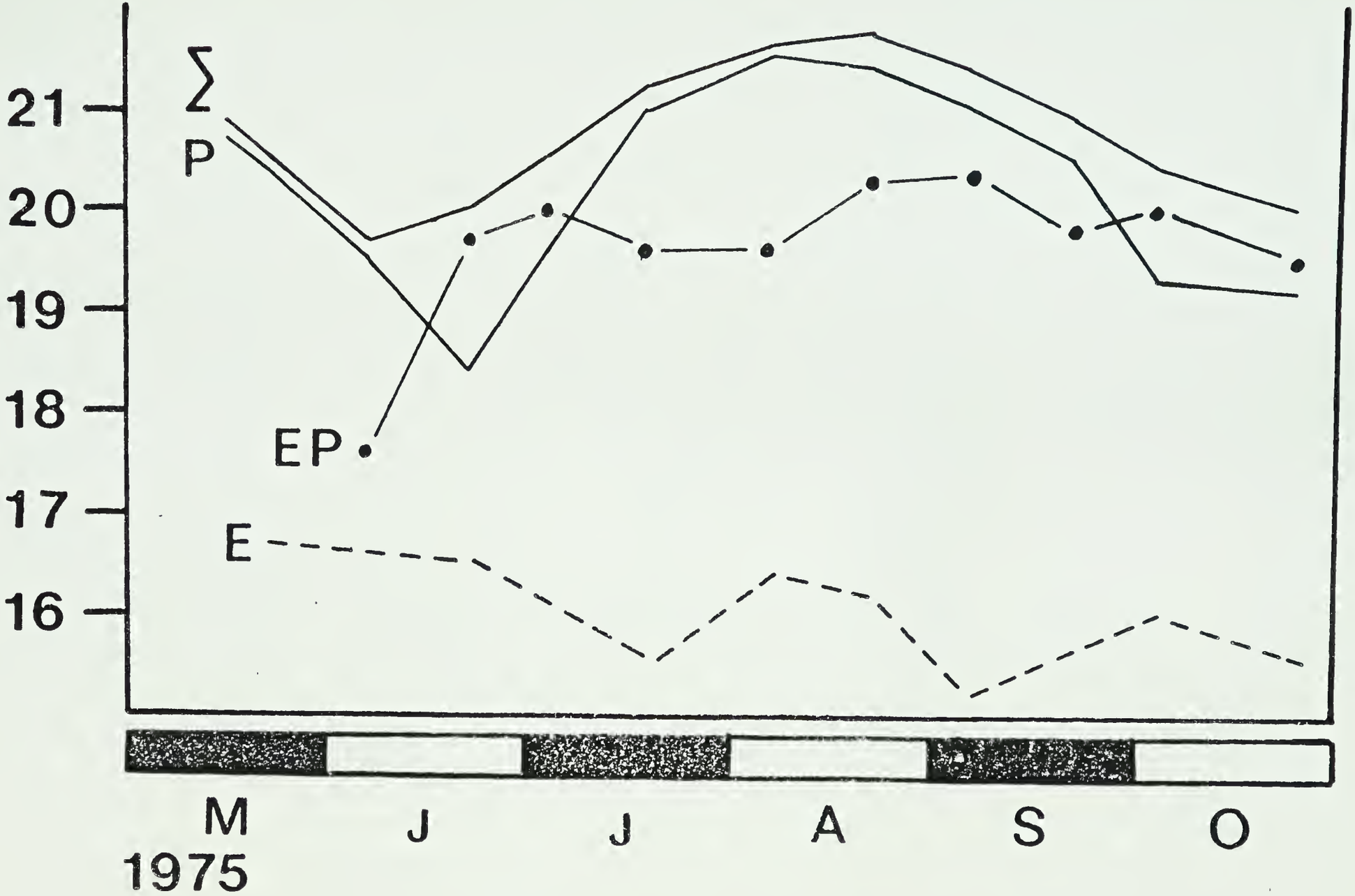

21
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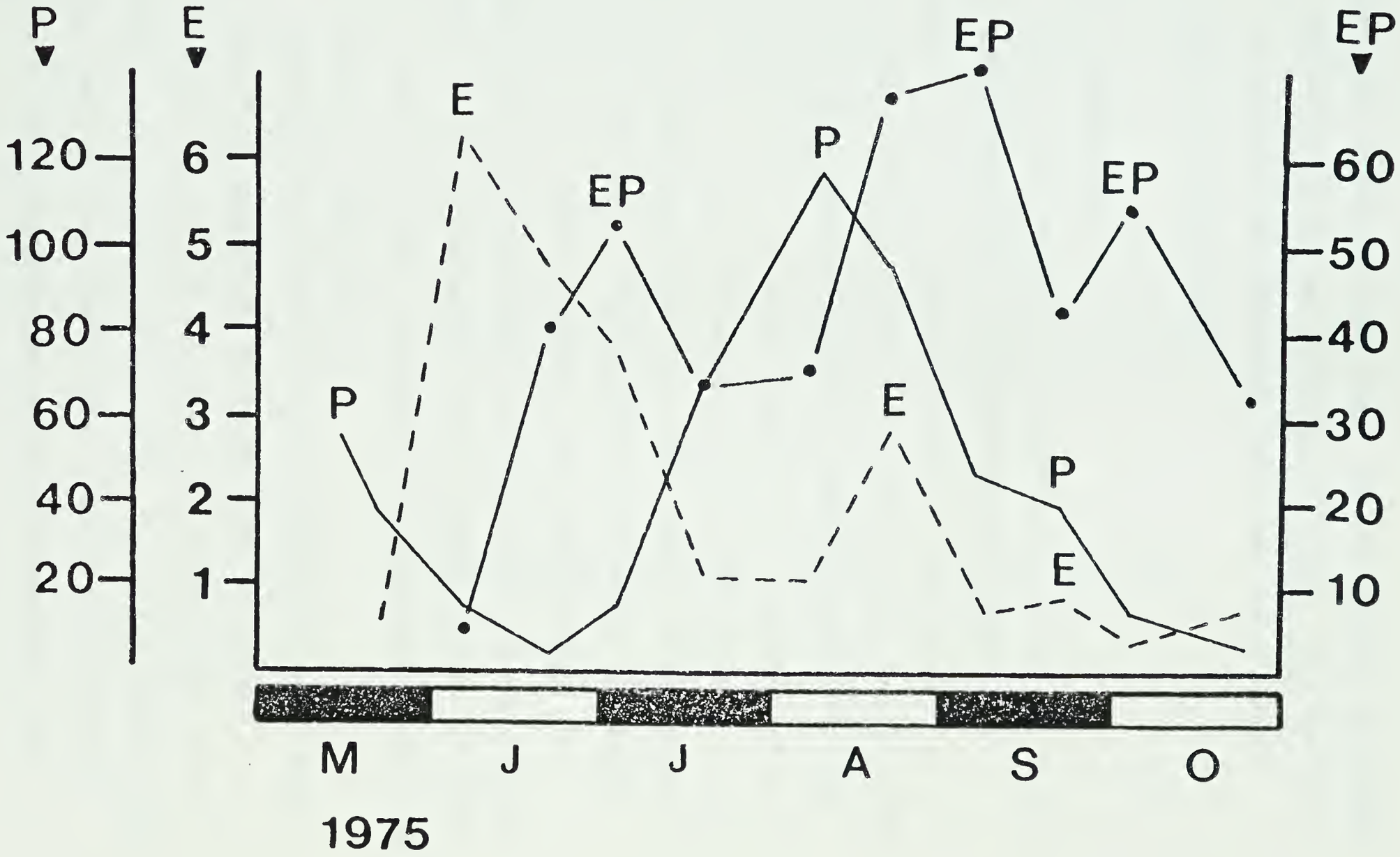
Figure 54.
Seasonal distribution of 0 m data for phytoplankton mg chlorophyll a/m^3 (_____), epipelon mg chlorophyll a/m^2 (-----), and epiphyton mg chlorophyll a/m^2 (._____.).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summer peaks followed the same order. During September and October the same ordered series was indicated for autumn. Data from 1974 and 1976 suggested the same series, but it was not so clearly delineated into seasonal sets.

6.1.4. Productivity

The vertical distribution of productivity for each of the three algal communities showed a marked decrease with depth (3.2.4. Productivity, 4.2.4. Productivity, 5.2.4. Productivity).

Productivity data based on 0 m collections were averaged (Table 14). The phytoplankton exhibited the greatest productivity, then the epiphyton, then the epipelon based on the respective per m^3 and per m^2 units. However, as was the case for standing crop, on a per m^2 lake surface basis in the 0-1 m depth interval of the littoral zone the productivity of the epiphyton was greatest. But again, distributed on a total lake format using two years data, the phytoplankton contributed 80%, the epiphyton 19%, and the epipelon 1% to total lake productivity. And the seasonal pattern for total lake productivity closely correlated with phytoplankton productivity ($r = 0.880$, $p > 0.025$)(Figure 55).

Indications of an ordered series of productivity peaks among the three algal communities were found based on 0 m data (Figure 56). During 1975 a spring series of phytoplankton, then epipelon, then epiphyton peaks occurred. This was followed by peaks in the same order for a summer series. However, for the autumn series an initial phytoplankton peak was not recorded, as the

Table 14. Productivity data for each algal community at 0 m, in the 0-1 m littoral zone, and on a total lake basis.

Productivity mg carbon hr^{-1} at 0 m	May-Oct. 1974	May-Oct. 1975	May-Oct. 1976
Phytoplankton m^{-3} water column	75	51	117
Epipelon m^{-2} sediment surface	6	2	2
Epiphyton m^{-2} host stem	19	43	28

Productivity mg carbon hr^{-1} in littoral zone 0-1 m depth interval	May-Oct. 1974	May-Oct. 1975	May-Oct. 1976
Phytoplankton m^{-2}	75	51	117
Epipelon m^{-2}	6	2	2
Epiphyton m^{-2}	179	405	264

Productivity kg carbon hr^{-1} in lake total	May-Oct. 1974	May-Oct. 1975	May-Oct. 1976
Phytoplankton	1300	865	722
Epipelon	52	13	13
Epiphyton	176	403	260
Summation	1528	1281	995

Figure 55.
Seasonal distribution of log 10 mg Carbon/hr
for total lake phytoplankton (_____),
total lake epipelon (-----),
total lake epiphyton (._____.), and
total lake summation (_____).

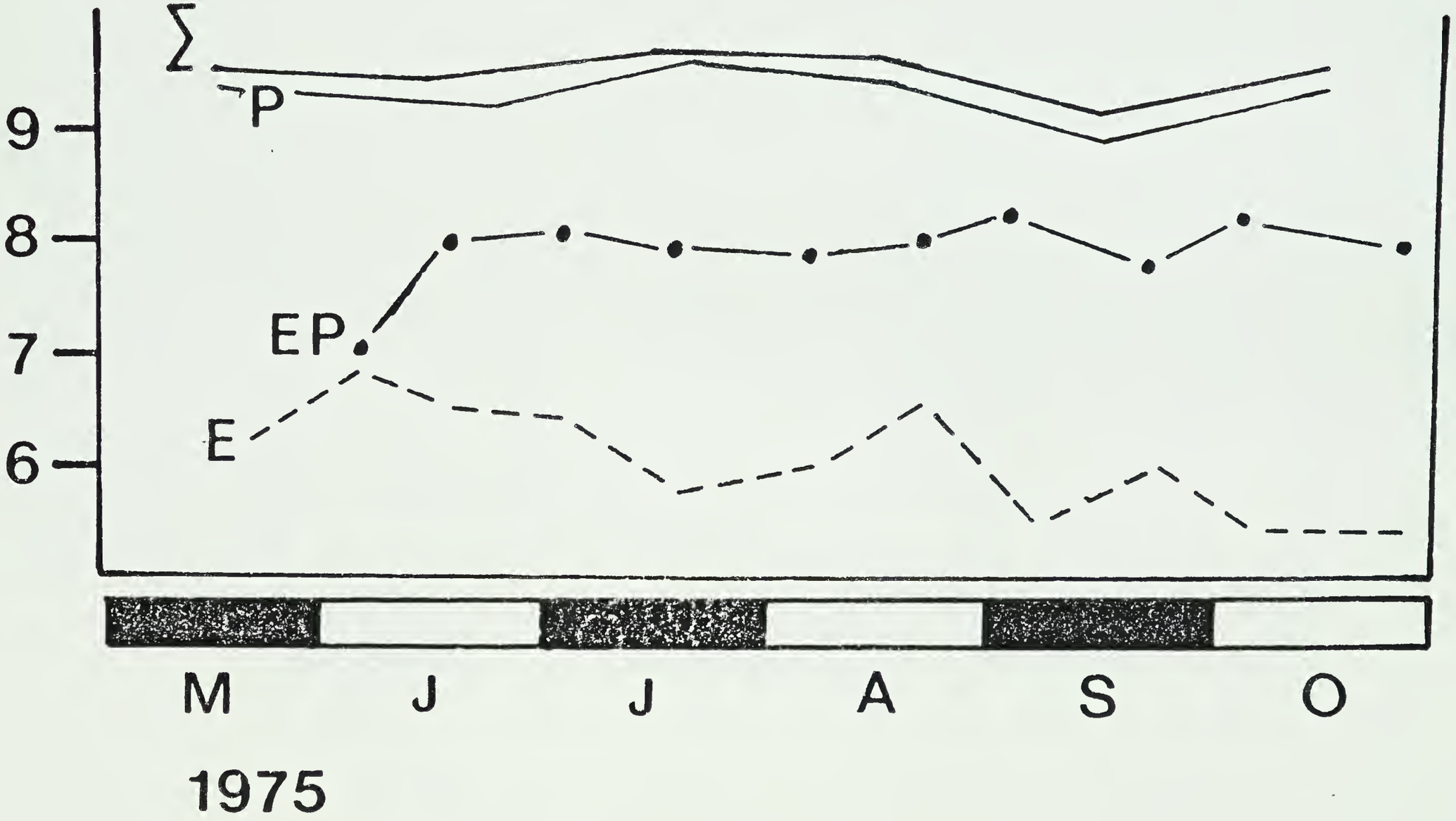
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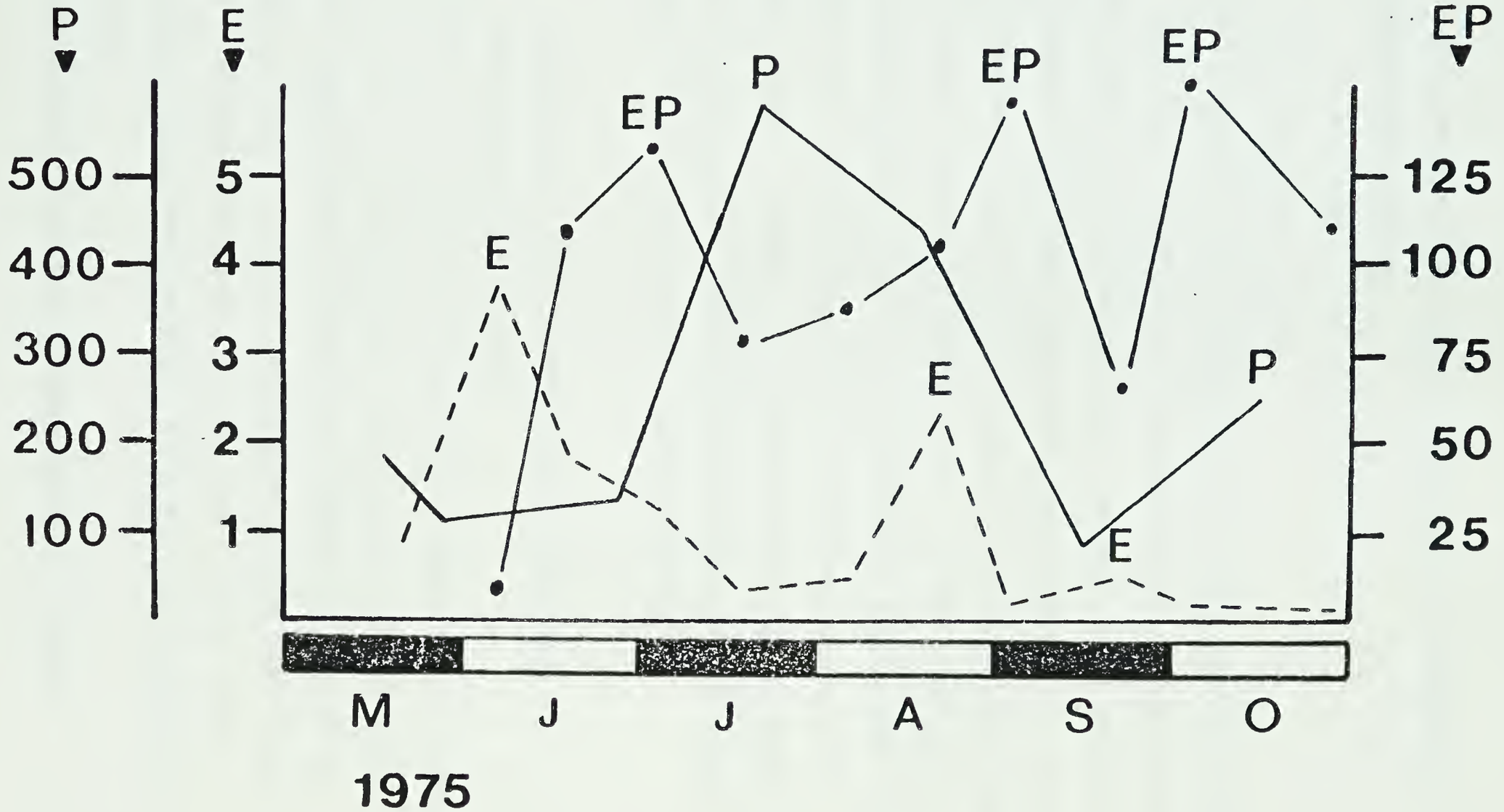
Figure 56.
Seasonal distribution of 0 m data for phytoplankton mg carbon/m^3/hr (_____), epipelon mg carbon/m^2/hr (-----), and epiphyton mg carbon/m^2/hr (._____.).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epipelon then the epiphyton peaked. Then before ice formation a phytoplankton peak occurred.

6.1.5. Cross Incubation Studies

Cross incubation studies noted active and senescent populations in all three algal communities. The spatial distributions of sun and shade adapted populations was found along the marked vertical distribution of light within each of the three communities. This carried over to the expression of sun and shade adapted populations during changes from season to season also. Both the phytoplankton and epiphyton showed indirect light inhibition as populations did not always show productivity increases as they were moved to the surface incubation. However, populations in the epipelon always did show an increase (3.2.5. Cross Incubation Studies, 4.2.5. Cross Incubation Studies, 5.2.5. Cross Incubation Studies).

6.1.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

Patterns of vertical distribution were similar for all three communities with the photosynthetic index decreasing with depth, while the photosynthetic efficiency and productivity efficiency increased with depth. However, patterns of seasonal distribution for the three communities were unclear (3.2.6., 4.2.6., 5.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency).

Quantitatively the phytoplankton yielded the highest

Table 15. Photosynthetic index, photosynthetic efficiency, and productivity efficiency for each algal community.

Photosynthetic Index	Range	Mean
Phytoplankton	0.50-11.10	4.13±2.71
Epipelon	0.10- 3.5	0.73±0.59
Epiphyton	0.20- 9.30	2.24±0.87

Photosynthetic Efficiency	Range	Mean
Phytoplankton	1.90-14.10	6.26±4.74
Epipelon	0.01- 0.07	0.03±0.03
Epiphyton	0.55- 6.67	2.64±1.62

Productivity Efficiency	Range	Mean
Phytoplankton	0.02- 0.60	0.09±0.04
Epipelon	0.01- 0.23	0.02±0.02
Epiphyton	0.01- 0.24	0.13±0.09

photosynthetic index and photosynthetic efficiency (Table 15). The epiphyton productivity efficiency was greatest. The epipelon results were considerably lower for each of the three productivity relationships.

6.2. Discussion

6.2.1. Physico-chemical Parameters

Incident radiation on Hastings Lake showed a marked seasonal aspect because of the lake's northerly latitude. In addition a marked vertical distribution of light was found with a mean depth of 2 m for the 1% irradiance level. During ice free periods, shading from the phytoplankton and from the detritus associated with the turbulent water column was evident (Ganf 1974a,b, 1975, Hickman 1979a,b,c). During periods of ice cover, ice and snow likewise reduced light penetration (Megard 1972). Also the growth and senescence of macrophytes produced further shading. Seasonal changes in the above factors resulted in the greatest penetration of light into the water column in spring and autumn. Still the rapid attenuation of light effectively restricted the euphotic zone in the pelagial portion of the lake to 0 to 2 m for the phytoplankton and in the littoral portion of the lake to 0 to 1 m for the epipelon and epiphyton. Thus the vertical distributions of light in Hastings Lake were notable lakewide and affected species, standing crop, and productivity distributions for all three algal communities.

In Hastings Lake the isothermal temperature conditions for the May through October period can also be associated with the turbulent

water column. This too may account for the quick heating and cooling during spring and autumn. From the perspective of this study, the well mixed nature of the lake provided the same temperature regime for all three algal communities for six months of the year. However, during November through April, some critical changes occurred. Inverse stratification set in, and although the vertical temperature gradient was not great, ice formed at the surface to a depth of approximately 75 cm. Thus the phytoplanktonic habitat was reduced by nearly 30% and most of the epiphytic habitat and shallow portions of the epipelic habitat were frozen solid in ice.

Vertical oxygen gradients were attributable to photosynthesis near the lake surface and decay near the lake bottom. Even so during the ice free seasons turbulent waters often distributed oxygen rather evenly throughout the water column. Mean seasonal oxygen concentrations were highest when spring and autumn productivity peaks occurred for each of the three algal communities. A summer decrease in mean oxygen indicated that although photosynthetic rates were high, total lake respiration and decomposition were proportionately higher. Low oxygen levels during winter were associated with low photosynthesis and active detrital decay.

The immediate response of pH and alkalinity to photosynthetic activity was interesting in that the vertical distribution of these two parameters persisted in spite of the well mixed water column during the ice free seasons. The former being positively associated

and the latter being negatively associated with productivity. These relationships were also expressed on a seasonal basis as high pH and low alkalinity resulted from high summer productivity in all three algal communities. Also, as the littoral zone was an area of intense photosynthetic activity for all three communities, the pH and alkalinity were respectively higher and lower as recorded for the epiphyton than for the other two communities.

Much of the silica in lakes is trapped in sediments (Harriss 1967). One then might expect a tendency toward higher concentrations in the epipelic habitat as was noted. However, high local concentrations can be found in macrophyte tissues which may serve as a major source of silica for the epiphyton (Harlin 1975). Seasonal fluctuations of silica have been linked to the periodicity of diatom populations (Lund 1964). But in Hastings, changes in silica could not be aligned with diatoms from any one of the three algal communities studied. It was only from a composite of all three communities that the full extent of the inverse relationship between diatoms and silica was shown.

The distribution of nitrate and orthophosphate in Hastings generally followed patterns found in eutrophic lakes (Wetzel 1975). Algal assimilation and nitrate reduction decrease nitrate concentrations and nitrification of organic matter increase concentrations. The complexity of the biotic and abiotic factors involved are shown as the amounts of nitrate available relative to each algal community studied were variable. But all communities did show nitrate increases in winter and decreases in summer.

Orthophosphate tended to increase whenever oxygen levels were low (Mortimer 1941, 1942, 1971) and whenever an active decomposition of organic matter occurred. Thus the highest concentrations of orthophosphate in Hastings were found in the epiphyton where a pool of terrestrial runoff, aquatic macrophytes, phytoplankton blooms, epiphytic algae, and epipelic algae collected and decayed (Nichols and Keeney 1973, Carpenter 1980, Boston and Perkins 1982, Landers 1982).

6.2.2. Species

Characteristic abiotic and biotic factors help define algal communities (Round 1965). Conditions associated with a given community then permit those algae better suited to those conditions to develop large populations. For example in Hastings Lake, Rhodomonas minuta formed large populations only in the phytoplankton; Navicula hungarica var. capitata formed large populations only in the epipelon; and Stigeoclonium nanum formed large populations only in the epiphyton. As conditions become inappropriate for growth, such populations are thought to senesce and to simply maintain themselves as a few viable individuals until favorable conditions periodically return within the respective communities. Thus a given species is often associated with a particular community (Moss and Karim 1969, Brown and Austin 1973, Kairesalo 1976). This is accepted as the general case for many species, and is one of the bases for the community concept (Round 1965a).

But for some Hastings species more complex intercommunity situations appear to exist. Even though a species may persistently maintain and develop large populations in one community, the bulk of the population may senesce in another community and so release large amounts of nutrients there (Boyd 1972); this was a situation noted in Hastings. And even though a species may develop large populations in a particular community, the species may be maintained in another community as inocula in very low amounts (Lund 1954); again a situation noted in Hastings. But of greater interest in Hastings were apparent situations in which a species first became a growing dominant population in a benthic community, then became a dominant in the phytoplankton, and finally became a dominant, but senescent, population in a benthic community. Although this may not be the general case for species (Round 1965a), it certainly had some merit with respect to certain Hastings species.

The epiphyton indeed may be a collection site for senescing phytoplanktonic blue-green populations for example, but it too may act as an incubator site where sufficient heat, light, and nutrients may initiate growth of populations that later develop to their fullest in the phytoplankton. The epipelon also may be considered a disposal site for senescent populations, but it too may be viewed as a stable maintenance site, where species may survive, or even display active growth.

The dominance of cyanophycean populations in Hastings indicated the lake's eutrophic status (Hutchinson 1967). This dominance was seen from community to community, suggesting more than just the

phytoplankton can be suitable for diagnosing trophic status (Besch, et al. 1972). In eutrophic lakes, physical parameters may seem more important than chemical parameters in determining biotic responses. Cyanophycean populations were able competitors when light and/or temperature were limiting and community biomasses were low. Likewise cyanophycean populations were able competitors when physical parameters were favorable, and nutrient rich waters were taxed by large community biomasses.

Diversity indices further elucidated community responses to environmental stress (Hill 1973, Peet 1974). High spring values tended to steadily give way to lower and lower values in summer, autumn, and winter. One may suggest that in spring small initial populations in each community took advantage of renewed physico-chemical conditions; abiotic and biotic stresses were low, and diversity was high. But as populations rapidly grew, physico-chemical parameters oscillated and biotic competition increased as biomass increased, thus biotic stress would lower diversities summer through autumn. Late in autumn when community biomass was still relatively high and on into winter when biomass was low, light and temperature decreased rapidly and so physical stresses increased. Diversity again decreased.

In general, the phytoplankton, then the epiphyton, then the epipelon showed high to low diversity indices in that order. This indicated the phytoplankton was under less environmental stress than the epiphyton, which in turn was under less stress than the epipelon. This was born out in standing crop (6.2.3. Standing

Crop) and productivity (6.2.4. Productivity) results for all three communities.

6.2.3. Standing Crop

Only a few studies which assess respective community contributions to standing crop in aquatic ecosystems have been done. The phytoplankton has been most frequently cited as the greatest contributor to total lake standing crop (Wetzel 1964, Moss 1968, 1969a, Adams and McCracken 1974, McCracken, et al. 1974, Kairesalo 1977). However, the epiphyton (Kowalczewski 1975) and the epipelon (Hargrave 1969) have been cited also.

Lake morphometry would be an important part of these results. As the surface area:volume ratio tends to be less, the contribution of the phytoplankton tends to be more. But as the ratio increases, the relative amount of substrate available in the photic zone increases and the benthic communities become more important.

In Hastings Lake the phytoplankton was the major community component for total lake standing crop, but the importance of the epiphyton was noted especially in the littoral zone. Seasonal data showed the total lake pattern to be closely aligned with that of the phytoplankton, but the epiphyton did have the largest standing crop lakewide during spring and autumn. The potential then for larger epiphytic standing crop seems limited only by available habitat.

The seasonal interplay of standing crop peaks among the three algal communities was of special note. The orderly sharing of a

temporal gradient by small and large biomass communities within an ecosystem has been noted in terrestrial studies. For example, many herbs flourish early in spring and late in autumn, small though their biomass may be, while the larger shrubs and trees develop during summer. This same sharing of time was seen in Hastings algal communities with a similar disparity of biomasses. Further discussion on the subject is provided in 6.2.4. Productivity.

6.2.4. Productivity

Intercommunity studies since the sixties have not only incorporated standing crop, but also productivity comparisons. Both the oxygen technique and the carbon-14 technique have been used to yield data on several communities within respective ecosystems. As was the case for standing crop comparisons, the phytoplankton has generally been found to have the highest productivity (Wetzel 1964, Hillbricht-Ilkowska, et al. 1972, Schindler, et al. 1973, Komarkova and Komarek 1975, Kairesalo 1980). But in other studies the epiphyton (Kowalczewski 1975) and the epipelon (Hargrave 1969, Hunding 1971) have been cited too.

These studies reflected the relative amount of community habitat available, and so stressed the importance of lake morphometry (Kerekes 1975). It has been suggested that the phytoplankton will be the major contributor to total lake productivity in deep lakes; whereas, the planktonic and benthic communities will yield approximately the same productivity in shallow lakes; and in shallow ponds, the benthic communities will be

largest (Wetzel 1975, Stanley 1976a,b).

Hastings is a relatively shallow lake with its long axis along the prevailing winds. The vertical distribution of productivity was closely linked to the 0-2 m photic zone. The phytoplankton made extensive use of the turbulent water column. That is, a large continuous biomass was circulated in and out of the 0-2 m depth interval throughout the total surface area of the lake. Movement through the water column also made available a more continuous pool of nutrients, avoiding local nutrient depletion. But benthic productivity was effectively restricted to the 0-2 m depth interval around the perimeter of the lake by attachment to substrates. However, it was these substrates that provided concentrated sources of nutrients. The phytoplankton then was the major component of total lake productivity in Hastings, but the epiphyton contributed substantially as was noted in the littoral zone.

Furthermore, seasonal aspects of productivity data showed qualitative interrelationships among the three algal communities apart from their relative quantitative contributions. Other studies have recognized the general similarity among the communities; spring, summer, and autumn peaks have been shown as environmental shock periods delineate seasonal sets (Round 1965a, 1971, 1972, Gargas 1972, Wetzel 1975). Also, there have been suggestions that respective community peaks will occur at different times within a season (Kowalczewski 1975, Kairesalo 1976), and that this timing may be attributed to genetic adaptations of major algal populations (Clark and Runnels 1975).

Indeed in Hastings, respective community productivity peaks did not overlap within seasons. As shock periods initiated new seasonal sets, the phytoplankton peaked first, then the epipelon, then the epiphyton. When given environmental parameters changed rapidly, or approached limiting levels, another shock period renewed the intercommunity cycle. This seral timing may reflect the evolution of community strategies minimizing competition and maximizing ecosystem energy utilization.

6.2.5. Cross Incubation Studies

The cross incubation studies illustrated qualitative similarities among the three algal communities. Within the spatial framework of each community a physical separation of active and senescent populations was found along a vertical gradient. These populations were often of different species. In addition each community showed a positioning of sun and shade adapted populations within their respective habitats. Thus, potentially active populations were in effect held in reserve to fluorish when new sets of environmental conditions were established between shock periods.

6.2.6. Photosynthetic Index, Photosynthetic Efficiency, and Productivity Efficiency

Patterns of vertical and seasonal distribution showed again qualitative similarities among communities. And in the case of the phytoplankton and the epiphyton, quantitative values seemed consistent with standing crop and productivity results (6.1.3.

Standing Crop, 6.1.4. Productivity). That is, the phytoplankton was the most active community, but the potential of the epiphyton was evident. Productivity relationships suggested the epipelon did not have the potential for being a major community quantitatively in Hastings unless there was a drastic increase in epipelic habitat and a drastic decrease in phytoplanktonic and epiphytic habitat.

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B30373